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THE INFLUENCE OF PRECIPITATION UPON THE WIDTH OF ANNUAL RINGS OF CERTAIN TIMBER TREES

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To the statistical personnel of the Section of Forest Measurements, United States Forest Service, fell the tedious, but nonetheless highly precise, work of making thousands of measurements of tree rings and performing the exacting computational tasks, which, at times, seemed enormous. Without this splendid support, the investigation would not have been undertaken.

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THE INFLUENCE OF PRECIPITATION UPON THE WIDTH OF ANNUAL RINGS OF CERTAIN TIMBER TREES

INTRODUCTION

Forest trees of temperate climates preserve their life histories in the records of their annual rings. From the record may be inferred the even-aged, or many-aged, character of the stand at the time of a tree's origin; the periods of suppression by neighboring trees or of dominance over them; the year of a forest fire or the year that a cutting may have been made in the immediate vicinity of a particular tree; perhaps, also, the years when weather had been particularly favorable, or detrimental, to annual ring growth.

But this is not all. If measurements of the widths of annual rings of a number of sample trees be arranged according to the sequence of years, it is possible to analyze the variation of the total set, and to assign, with more or less accuracy, the several portions to their causes, or groups of causes, such as the following:

(1) A portion due to differences among the trees within the stand. It is made up of variation among the average growth rates of the individual trees over the period of investigation.

(2) A portion whose causes are common to all the trees of the stand. It is made up of variation among average ring widths in different years and is itself divisible into (a) a part due to slow changes in average growth rate associated with the longer time adjustment of trees to changes in environment or to advancing age; and (b) a part due to variation from year to year depending upon weather during and preceding the growing season.

(3) A residual portion due to unaccounted-for variation.

The second part of the portion whose causes are common to the trees of the stand should, ideally, form statistically homogeneous material for the study of meteorological effects. That it need not contain the bulk of the contribution of the total complex of factors which influences timber growth is indicated by the analyses of 756 observations, made by Schumacher and Meyer (1937) on 12 white fir trees from a Swiss stand over a period of 63 years, for which assignable causes make up the following percentages of the total sum of squares of deviations from the general mean:

Variation among the individual trees, including slow changes	65.3	percent
Common annual variation	20.1	"
Residual, unaccounted-for variation	14.6	"

In this case, only 20 percent of the total is in annual variation. The need for isolating it from the remaining extraneous portions in order to investigate the influence of weather on timber-tree growth is evident.

It is the purpose of the present paper to report an investigation of annual ring widths of each of several timber species indigenous to regions of the eastern United States. It consists of two parts: (1) The isolation of what are believed to be statistically homogenous observations made up of annual variation of tree-ring widths, freed from slow change in growth rate and from individual tree effects; and (2) a study of the influence of a single meteorological factor, precipitation, upon this annual variation.

THE TREE DATA

The data consist of measurements of annual ring widths according to calendar years for which United States Weather Bureau records list monthly precipitation at nearby stations. Two or more measurements were taken on each ring with a microscope-caliper[3] to a least count of 0.01 mm. Pertinent, available information of a general nature concerning the tree ring data is as follows:

(1) White oak (*Quercus alba* L.), 9 miles from the rain gauge at Asheville, North Carolina; 17 dominant and codominant trees of average age 185 years and a range of 71 to 325; average d.b.h.[4] of 23 inches, and range of 17 to 35; 4 measurements of each annual ring for the years 1904 to 1935, on cross-cuts at from 15 to 17 feet above ground. When the measurements of these trees were plotted, they were sorted into two groups solely according to ocular estimate of the residuals from estimated tree trends (Fig. 1). The order of residuals seemed higher in the case of tree numbers 1 to 12, than in tree numbers 13 to 17. On the supposition that significant differences might be uncovered between these groups, they were kept separate.

(2) Three groups of longleaf pine (*Pinus palustris* Mill.) from Florida. (a) 12 dominant trees, 2 miles from the rain gauge at Lake City (Fig. 2); average age 32 years from an even-aged stand; average d.i.b.[5] taken on 12- to 18-inch stump heights, 10 inches, with a range of 8 to 13; 4 measurements of each annual ring of the years 1908 to 1935, on cross-cuts at stump. (b) 18 dominant and codominant trees, 4 miles from the rain gauge at Gainesville (Fig. 3); average age 50 years and ranging from 45 to 62, from an approximately even-aged stand; average d.i.b. on 12- to 18-inch stumps, 12 inches and ranging from 8 to 16 inches; 4 measurements of each annual ring of the years 1894 to 1935 on cross-cuts at stump. (c) 12 dominant and codominant trees, 7 miles from the rain gauge at Jacksonville (Fig. 4); average age 58 years and ranging from 45 to 80 years; average d.i.b. on 12- to 18-inch stumps, 11 inches, with a range of 8 to 14; 4 measurements of each annual ring of the years 1894 to 1935 on cross-cuts at stump.

(3) Two groups of shortleaf pine (*Pinus echinata* Mill.) from Virginia, 10 miles from the Weather Bureau station at Washington, D. C., represent-

[3] The instrument used was designed by the Division of Forest Entomology of the Bureau of Entomology and Plant Quarantine. It consists of a binocular with a carefully machined moving stage and micrometer. It works accurately and rapidly.

[4] Diameter breast high.

[5] Diameter inside bark.

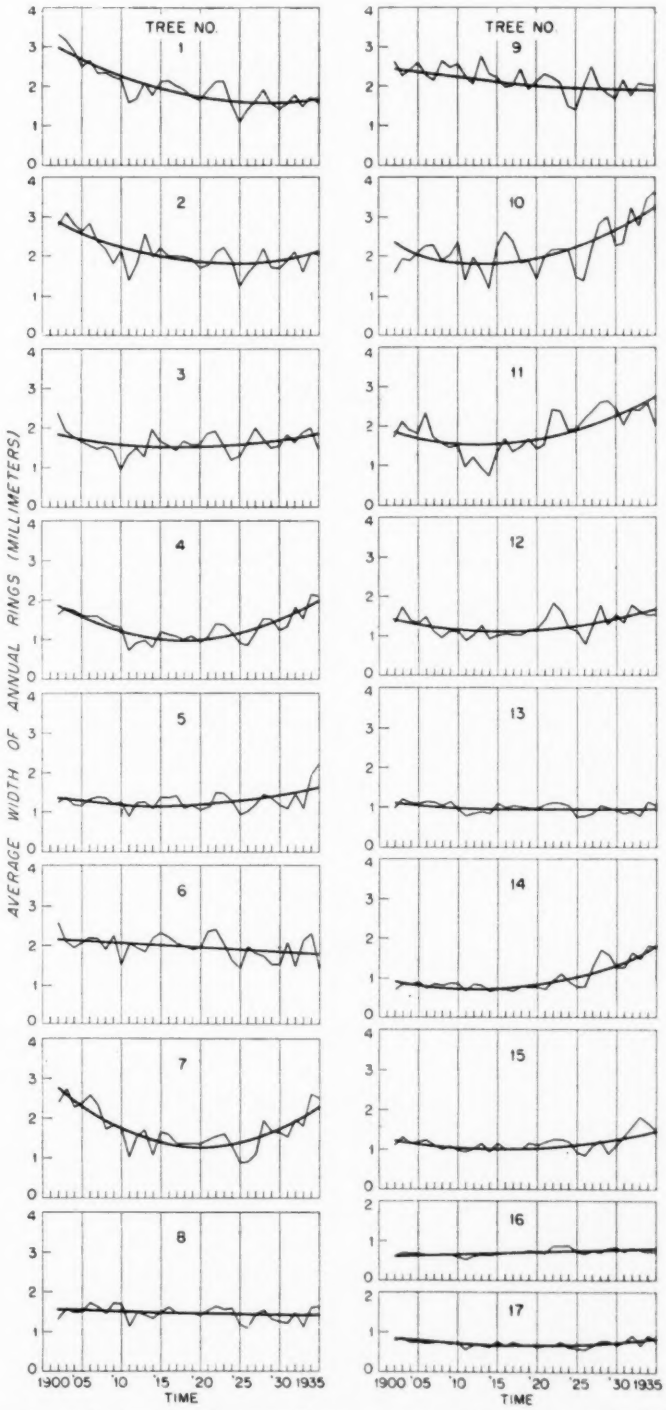

FIG. 1. Annual ring width according to tree and year, and individual tree trends of white oak near Asheville, North Carolina.

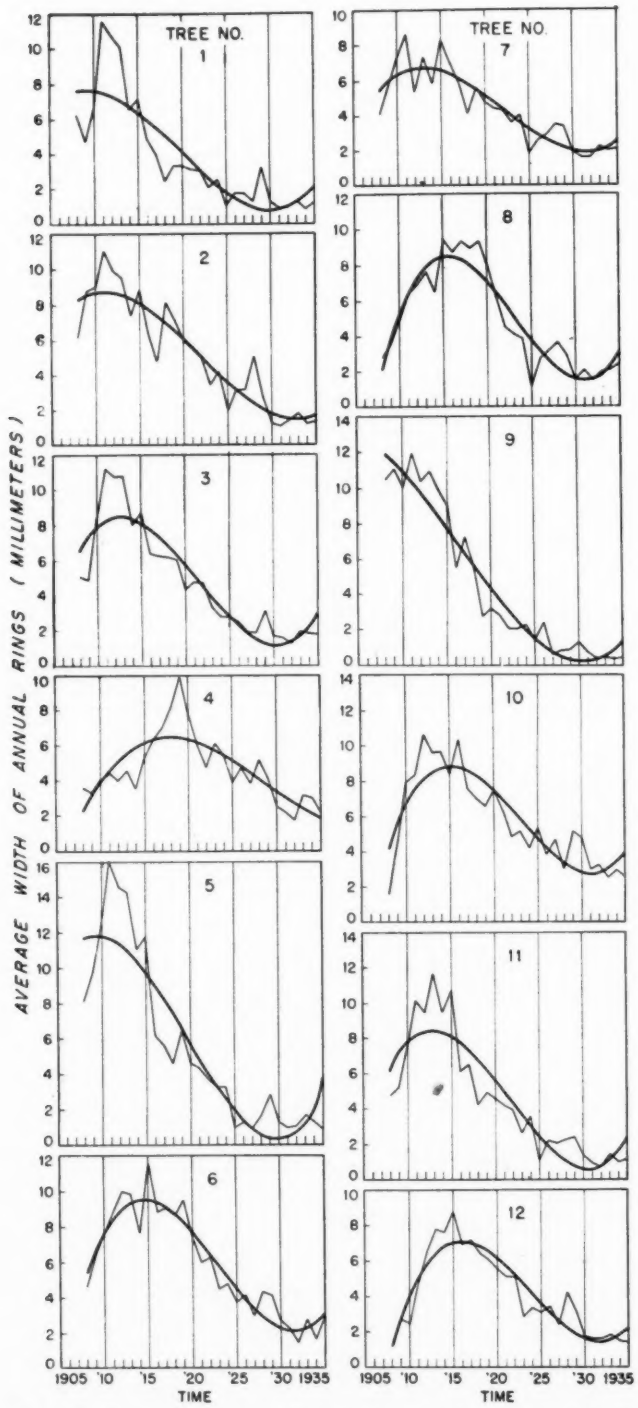

FIG. 2. Annual ring width according to tree and year, and individual tree trends for longleaf pine near Lake City, Florida.

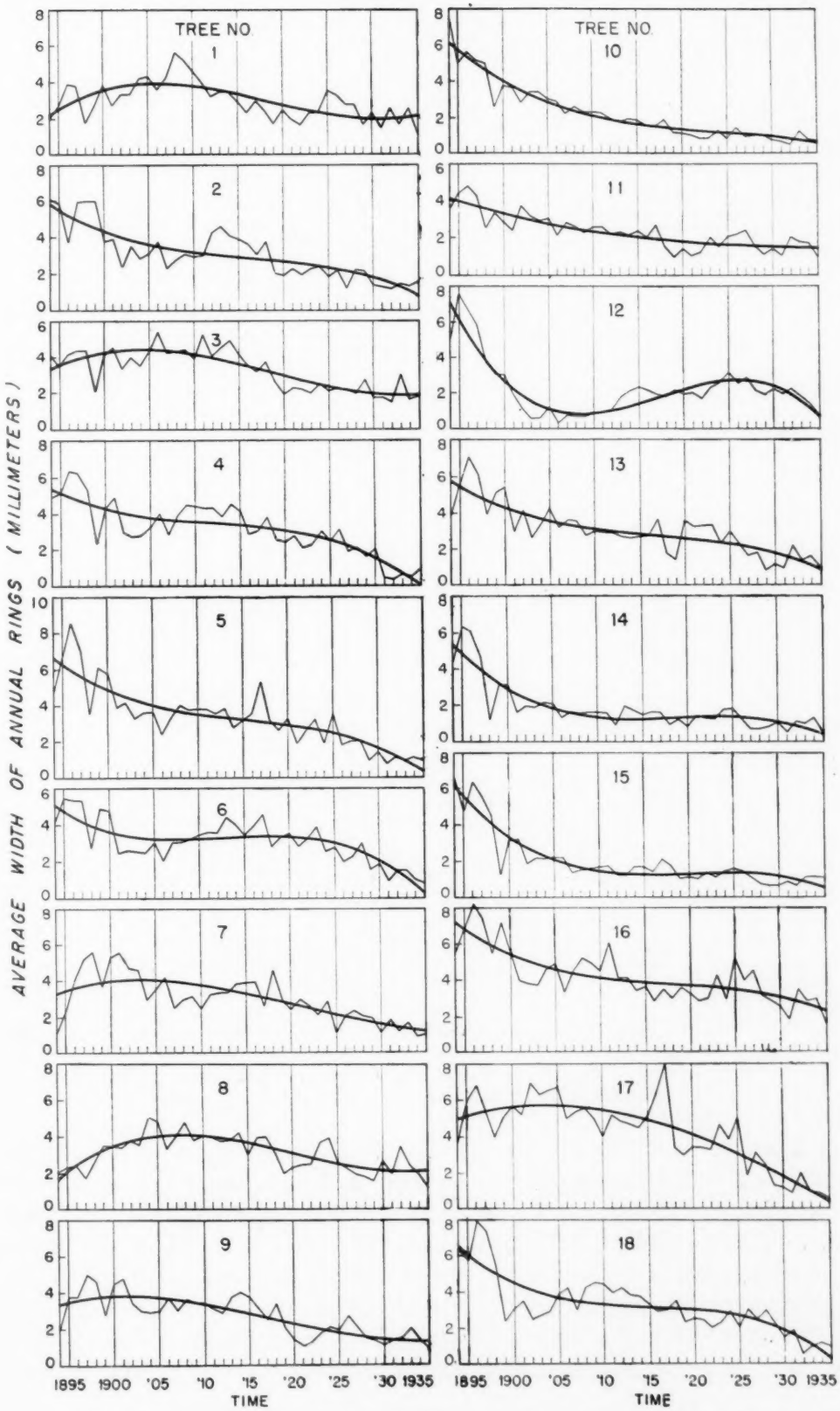

FIG. 3. Annual ring width according to tree and year, and individual tree trends for longleaf pine near Gainesville, Florida.

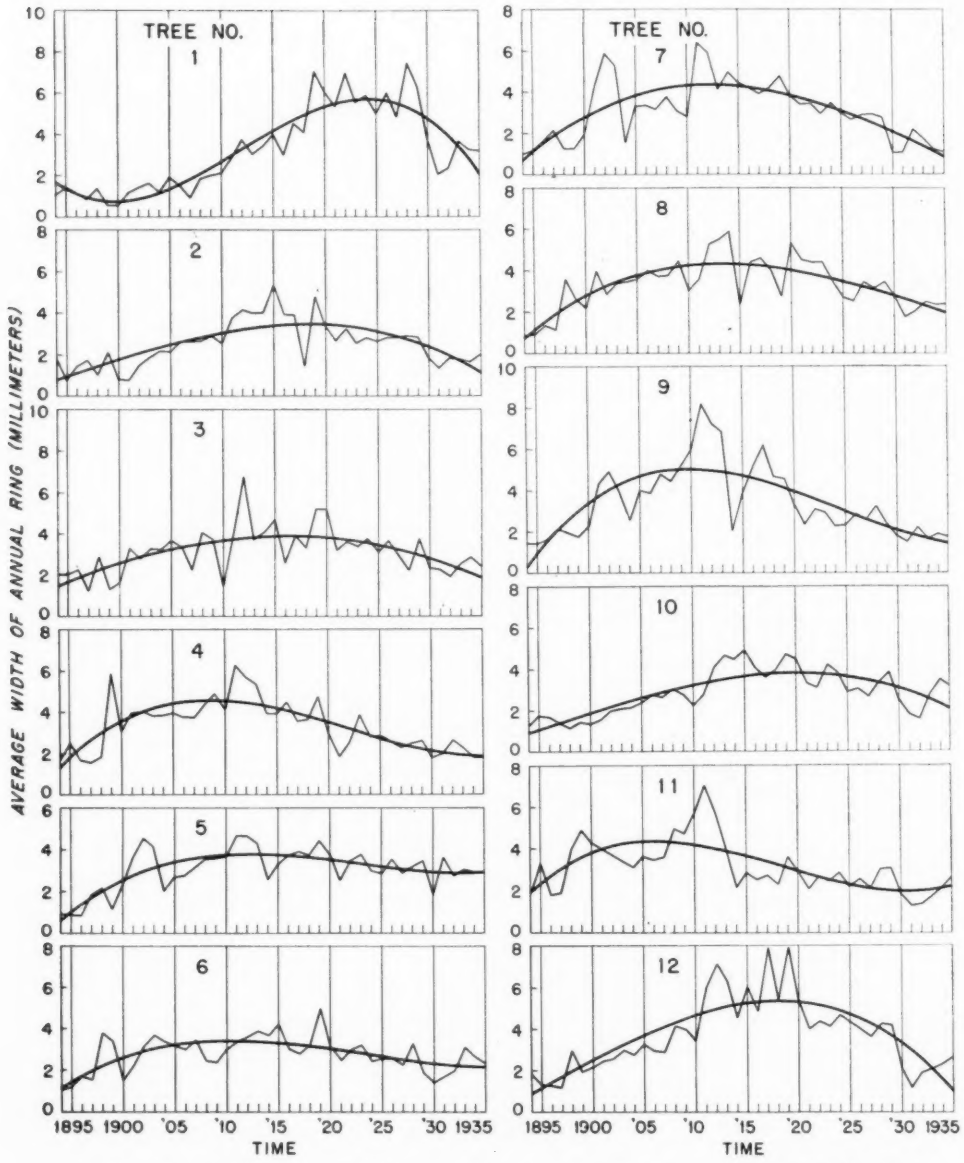

FIG. 4. Annual ring width according to tree and year, and individual tree trends for longleaf pine near Jacksonville, Florida.

ing 2 stands of the same forest. (a) 14 dominant and codominant trees which had been growing in an even-aged stand on a lower slope; 80 to 85 years of age in 1933, when the trees were attacked by bark beetles; average d.i.b. on 2-foot stumps, 10 inches, with a range of 7 to 14; 2 measurements of each annual ring of the years 1854 to 1932 on cross-cuts from stump. As all the trees died before 1934, this group is distinguished by the designation "Dead trees" (Fig. 5). (b) 15 dominant and codominant trees on a middle slope in an approximately even-aged stand of 65 to 80 years; average

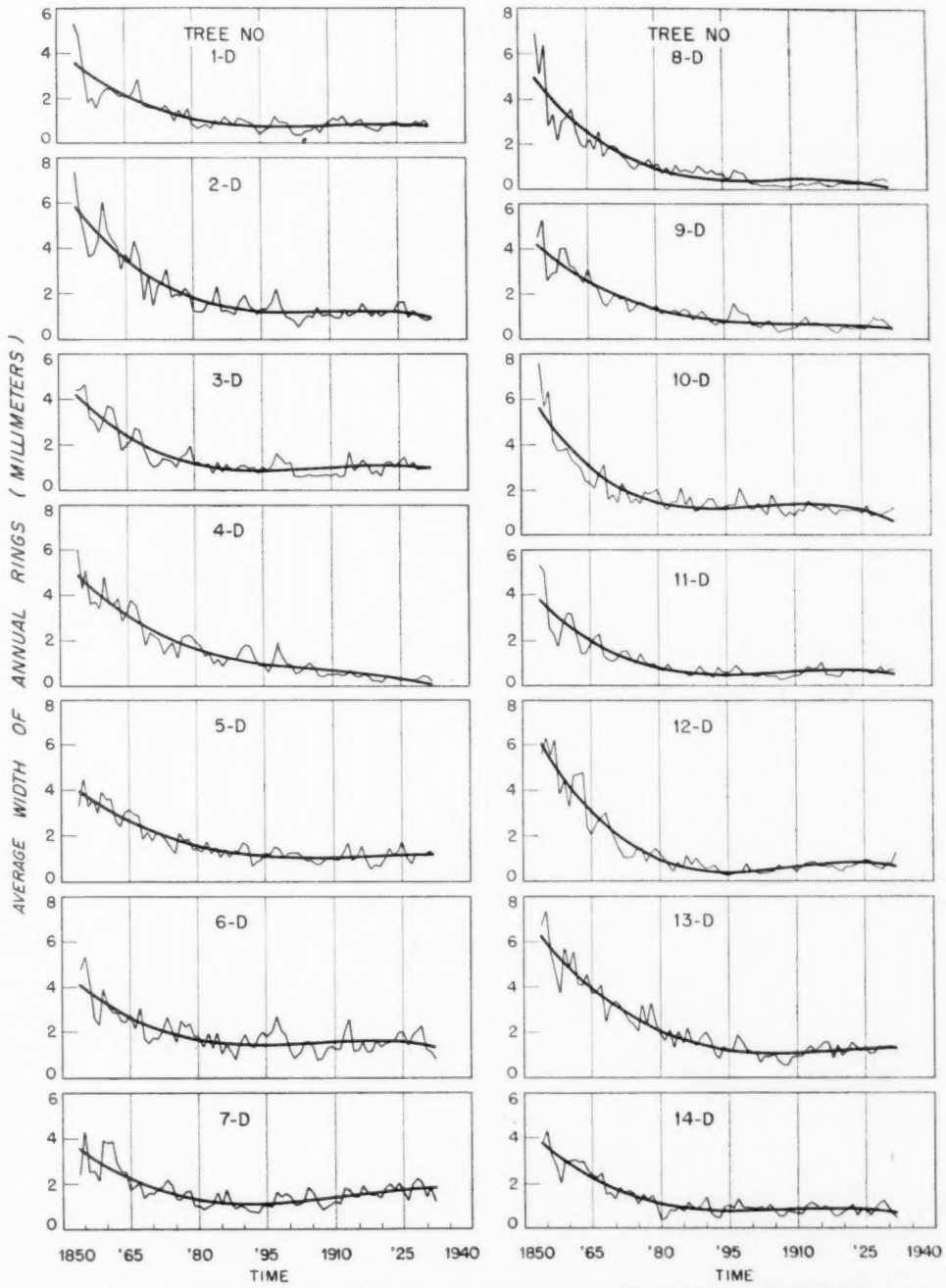

FIG. 5. Annual ring width according to tree and year, and individual tree trends for shortleaf pine in Virginia, near Washington, D. C. "Dead" tree group.

d.i.b. on 2-foot stumps, 11 inches, and ranging from 8 to 15; 2 measurements of each annual ring of the years 1874 to 1935 on cross-cuts from stump. As these trees showed no effect of the bark beetle attack of 1933, they are designated "Live trees" (Fig. 6).

(4) One group consisting of 8 trees of hemlock (*Tsuga canadensis* (L.), Carr.) from near Hanover, New Hampshire (Fig. 7). The original measurements on these trees were very kindly placed at the disposal of the authors by Dr. Charles J. Lyon who had collected them for another investigation. Concerning the site Lyon (1936, p. 462) states:

> Hanover. This site was a wood-lot with a rough terrain of ridges and hollows at an elevation of about 700 feet. The airline distance to the Weather Bureau cooperating station at Dartmouth College is about 2 miles, without appreciable differences in altitude. The eight trees were located within an area of a few acres but with all ranges of habitat from low ridge crest to the margin of a summer-day swamp trough. ——the area appeared to have been the scene of selected cuttings of trees at various intervals during the 19th century, so that the dates of release of the small hemlocks were not the same for any two trees sectioned for this study.

The average age of all the trees in Lyon's investigation was 279 years and only one section had less than 200 rings. Annual ring widths were measured along three average radii each, and the mean of the three taken as an index of the growth rate for the year. These measurements are for the years 1835 to 1934. The Weather Bureau rainfall records are missing for the interval 1856 to 1867.

THE ISOLATION OF ANNUAL VARIATION

The raw data, that is the average of the two, three, or four measurements of each ring are presented graphically in Figures 1 to 7, according to tree-year classification. There is a separate figure for each of the groups described above. The individual trend curves shown with the data of each tree are not pertinent to the discussion below, because examination of the graphical representation indicates that trend curves of the same degree should fit all trees of a group. Hence instead of fitting as many curves as there are trees, and averaging the residuals according to years, the same result is achieved by fitting a trend to the average ring width of all trees of a group according to the year in the sequence, and using the residuals from this average trend.

The first problem is the analysis of the total variation of the ring widths of each group of trees into contributing portions. Given the following definitions:

y_{ij} the measured width of the annual ring of a particular year i out of the n years of the sequence, on tree j from among the k trees of the group;
m_i the mean of the k ring widths in year i;
t_j the mean of the n ring widths on tree j;
m the general mean width of all nk rings.

Then the deviation of an annual ring width from the general mean of the group may be expressed

$$(y_{ij} - m) = (m_i - m) + (t_j - m) + (y_{ij} - m_i - t_j + m)$$

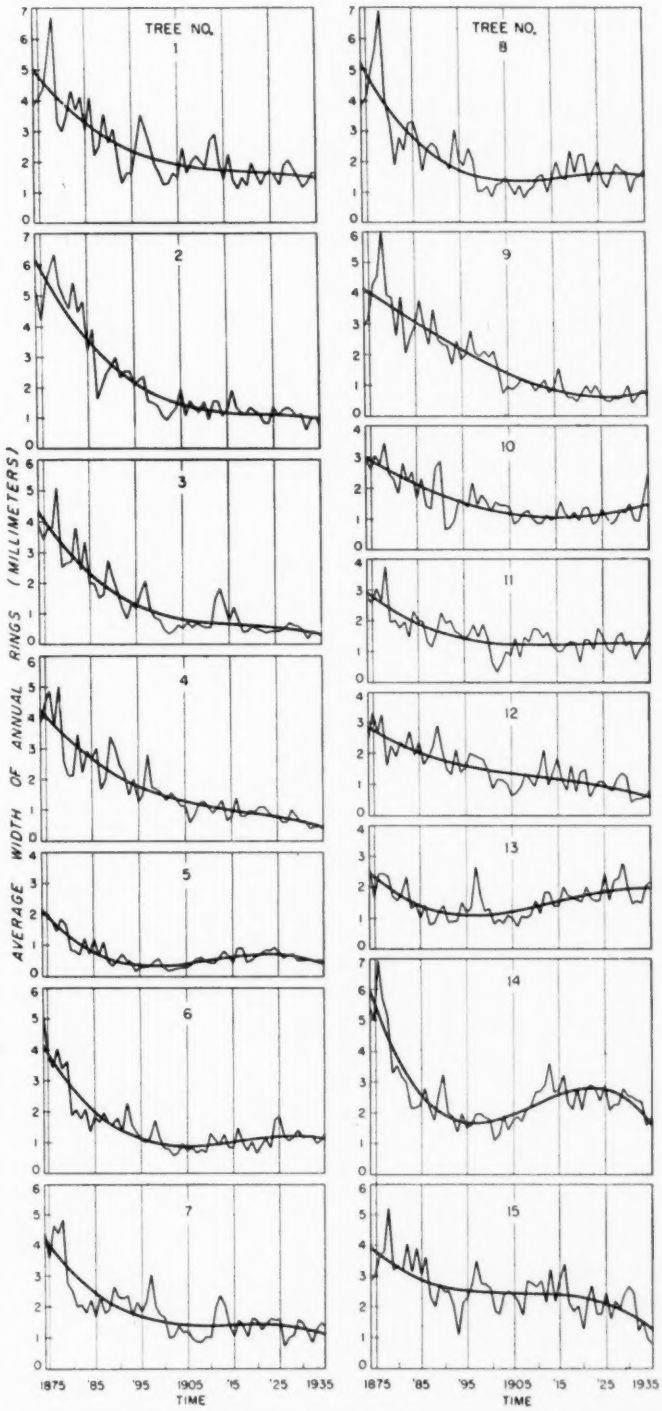

FIG. 6. Annual ring width according to tree and year, and individual tree trends for shortleaf pine in Virginia, near Washington, D. C. "Live" tree group.

for which the three terms of the right-hand member represent the year i effect, the tree j effect, and the residual, respectively. Upon squaring and adding over all n rings of one tree we have

$$\sum_{1}^{n}(y_{ij}-m)^2 = \sum_{1}^{n}(m_i-m)^2 + n(t_j-m)^2 + \sum_{1}^{n}(y_{ij}-m_i-t_j+m)^2$$

and after adding like terms for all k trees, the total sum of squares is

$$\sum_{1}^{k}\sum_{1}^{n}(y_{ij}-m)^2 = k\sum_{1}^{n}(m_i-m)^2 + n\sum_{1}^{k}(t_j-m)^2 + \sum_{1}^{k}\sum_{1}^{n}(y_{ij}-m_i-t_j+m)^2 \ldots\ldots (1)$$

The left-hand member of this identity is the total sum of squares and the right-hand member contains its division into portions which are due, in order, to differences among years, among trees, and to the remaining unaccounted-for variation. As disclosed by the data (Figs. 1 to 7) however, the sum of squares among years—that is, $k\sum_{1}^{n}(m_i-m)^2$—is not yet to be considered as made up of statistically homogeneous material. It is still encumbered by any effects of slow change of growth rate which may be common to all the trees of the group. The latter may be removed upon fitting time trend curves to express such slow change.

Polynomials of sufficiently high degree were fitted to each group, by the method of least squares, so as to give residuals with approximately zero trends. These are shown in Figures 8 to 11. The trend curves of the oaks are of second degree; shortleaf pine in Virginia and longleaf pine at Jacksonville, of third; longleaf pine at Lake City, fourth; at Gainesville, sixth; and hemlock at Hanover, New Hampshire, tenth.

Denoting by c_i the estimate of m_i in any year as given by the trend curve, fitted according to the method of least squares, then

$$k\sum_{1}^{n}(m_i-m)^2 = k\sum_{1}^{n}(m_i-c_i)^2 + k\sum_{1}^{n}(c_i-m)^2$$

in which the first term of the right-hand member is the sum of squares due to annual variation of ring width, free from the effect of slow changes whose sum of squares make up the second term.

Upon substituting the right-hand member of this identity into equation (1), the whole is conveniently converted into analysis of variance form as in Table 1. The residuals from the average trends, according to year of growth and tree group are the data upon which the investigation of the influence of the single meteorological element, precipitation, is based. Their sum of squares is expressed algebraically in Table 1, third line from the bottom.

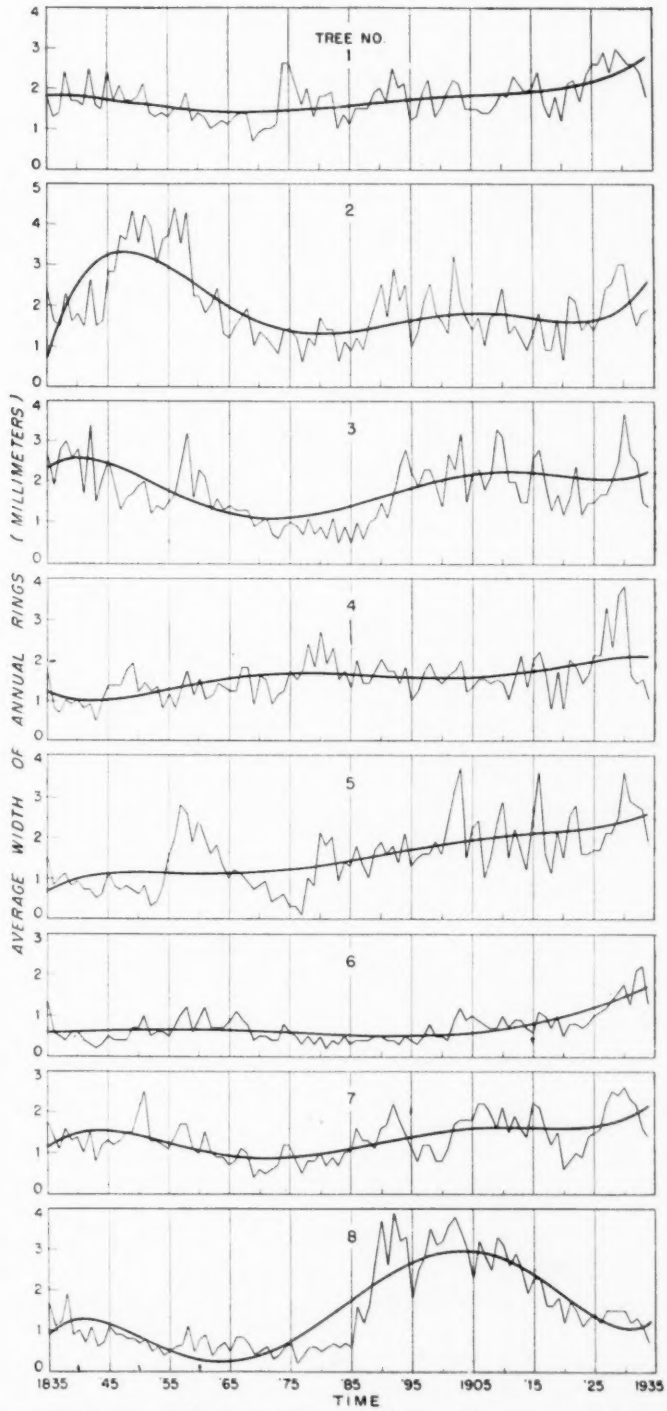

FIG. 7. Annual ring width according to tree and year, and individual tree trends for hemlock near Hanover, New Hampshire.

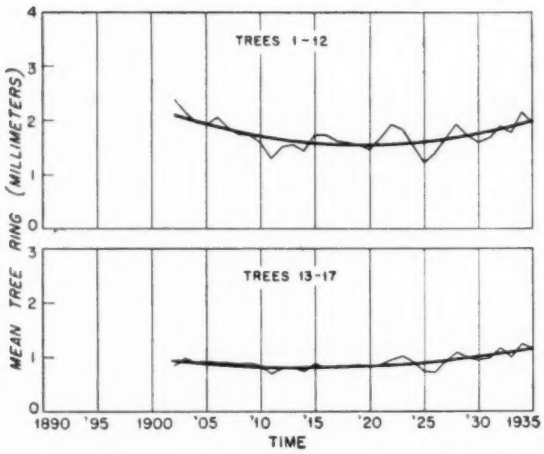

FIG. 8. Average annual ring width of white oak trees according to tree group and year, and trend curves of degree 2 fitted thereto.

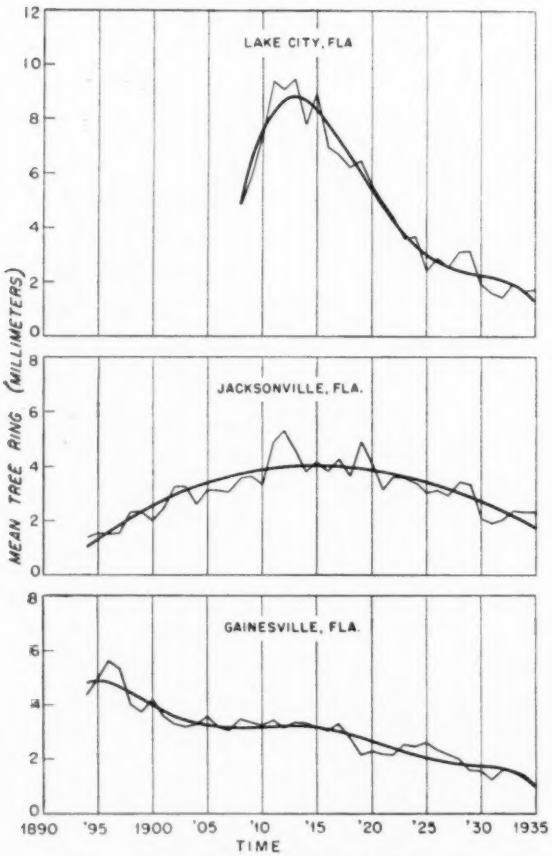

FIG. 9. Average annual ring width of longleaf pine trees according to locality and year, and trend curves fitted thereto. The trend curve of the Lake City group is of degree 4; of the Jacksonville group, degree 3; and of the Gainesville group, degree 6.

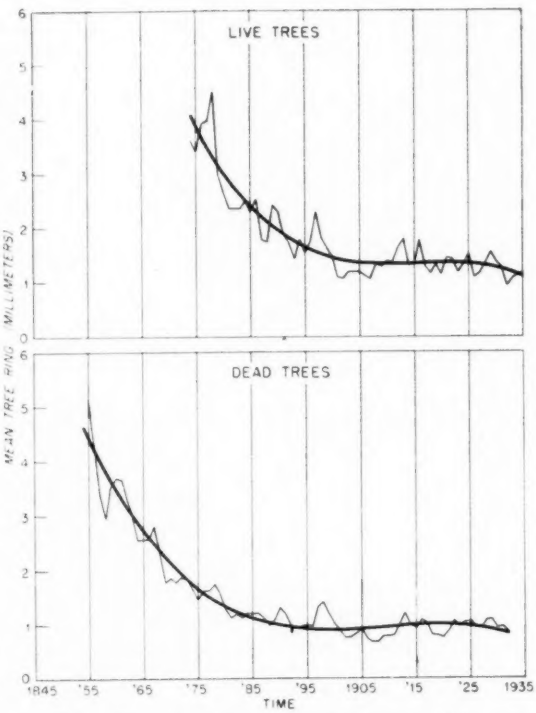

FIG. 10. Average annual ring width of shortleaf pine trees according to tree group and year, and trend curves of degree 3 fitted thereto.

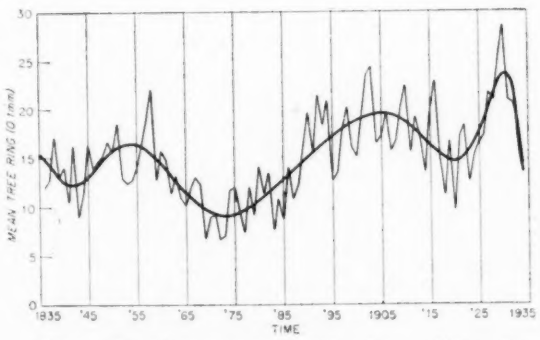

FIG. 11. Average annual ring width of hemlock trees according to year, and trend curve of degree 10 fitted thereto.

TABLE 1. DIVISION OF SUM OF SQUARES OF TREE RING WIDTHS INTO PORTIONS DUE TO ASSIGNABLE CAUSES

Variation due to	Sum of squares
Between tree means	$u\sum_{1}^{k}(t_j-m)^2$
Between years:	
Average trend (slow change)	$k\sum_{1}^{n}(c_i-m)^2$
Residuals from trend	$k\sum_{1}^{n}(m_i-c_i)^2$
Unaccounted-for remainder	$\sum_{1}^{k}\sum_{1}^{n}(y_{ij}-m_i-t_j+m)^2$
Total	$\sum_{1}^{k}\sum_{1}^{n}(y_{ij}-m)^2$

WHITE OAK IN NORTH CAROLINA

Table 2 shows the division of the sum of squares of the white oak data according to the scheme of Table 1. Two new columns are added, one containing the degrees of freedom, or number of independent comparisons, upon which each sum of squares is based, and the other containing the proportions, in percentage of total sum of squares, according to the source of variation.

This last column brings out clearly that the width of an annual ring among these oaks is governed to a much greater extent by the nature of the tree and the long-time environment of its immediate situation than it is by the annual fluctuations of weather. The effects of the former two causes appear in the proportions between tree means, and these make up more than 40 percent of the total. Slow changes in growth, common to all the trees, and expressed in this case by the trend curve of degree 2, is ascribable, it would seem, to slow changes of site quality— since the tree ages are so variable—account for 12 to 15 percent. The annual variation, on the other hand, the causes of which are ascribed to variation of meteorological factors from year to year, makes up only 9 to 12 percent.

These observations are not meant to imply that the effects of weather are negligible. They indicate, rather, that the data in the aggregate are extremely heterogeneous. If we consider only the more homogeneous variation among the residuals from trends, the proportion due to annual variation is $\frac{12.1}{12.1+33.9}$ or 26 percent for the first twelve trees; and $\frac{8.5}{8.5+32.5}$ or 21 percent for the remaining five trees.

The residuals from the average trend of the white oak data of Figure 8, according to year of growth and tree group, are given in Table 3. These are

TABLE 2. DIVISION OF WHITE OAK SUMS OF SQUARES INTO PORTIONS DUE TO ASSIGNABLE CAUSES. BENT CREEK EXPERIMENTAL FOREST, ASHEVILLE, N. C. UNITS OF HUNDREDTH MILLIMETERS SQUARED.

Due to	Trees 1-12			Trees 13-17		
	Degrees of freedom	Sum of squares	Percentages of total	Degrees of freedom	Sum of squares	Percentages of total
Between tree means	11	379,243	42.1	4	46,863	44.3
Between years:						
Average trend (slow change)	2	106,788	11.9	2	15,512	14.7
Residuals from trend	29	108,518	12.1	29	9,028	8.5
Unaccounted-for remainder	341	305,217	33.9	124	34,278	32.5
Total	383	899,766	100.0	159	105,681	100.0

TABLE 3. RESIDUALS FROM THE AVERAGE TREE TREND OF EACH GROUP ACCORDING TO YEAR OF ANNUAL RING GROWTH IN UNITS OF 0.01 MM. WHITE OAK, BENT CREEK EXPERIMENTAL FOREST, ASHEVILLE, N. C.

Trees 1 to 12				Trees 13 to 17			
Year	Residual	Year	Residual	Year	Residual	Year	Residual
1904	— 1.75	1920	— 7.25	1904	— 0.20	1920	— 0.40
1905	0.83	1921	13.42	1905	3.40	1921	1.20
1906	18.75	1922	37.08	1906	2.40	1922	10.00
1907	4.50	1923	27.00	1907	3.40	1923	13.60
1908	— 3.58	1924	— 7.33	1908	0.60	1924	2.80
1909	— 0.92	1925	—38.17	1909	5.00	1925	—15.80
1910	—10.25	1926	—24.50	1910	— 0.80	1926	—20.40
1911	—38.50	1927	2.50	1911	—12.80	1927	— 1.40
1912	—11.92	1928	24.42	1912	— 1.80	1928	12.20
1913	— 6.33	1929	0.67	1913	1.20	1929	0.08
1914	—15.25	1930	—15.42	1914	— 7.40	1930	— 6.20
1915	15.50	1931	—11.50	1915	5.80	1931	— 5.00
1916	17.08	1932	5.75	1916	— 1.80	1932	9.20
1917	6.75	1933	—11.08	1917	2.00	1933	— 9.60
1918	3.83	1934	21.33	1918	0.40	1934	11.00
1919	1.25	1935	— 5.17	1919	3.20	1935	— 1.80
General mean: 170.97				General mean: 91.36			

data upon which the investigation of the influence of the single meteorological element, precipitation at Asheville, North Carolina, is based.

LONGLEAF PINE IN FLORIDA

In Table 4 is presented the division of the sum of squares of the longleaf pine data for each of the three localities. A relatively minor part of the variation is due to differences among means, amounting to 4, 17, and 5 percent, respectively, for the data from Lake City, Gainesville, and Jacksonville.

On the other hand, slow changes in growth account for considerably greater portions, these being 68, 44, and 37 percent of the group totals. However, as the data of each group are approximately of even age, the average trends undoubtedly represent the longer-time effect of advancing age as well as slow changes of site quality.

The annual variation is, again, relatively little, comprising from 3 to 12 percent of the group totals. Of the more homogeneous variation, the annual variation makes up 10, 12, and 20 percent, according to the groups in order.

The residuals from average trends of the longleaf pine data of Figure 9 are listed in Table 5 according to year and tree group.

SHORTLEAF PINE IN VIRGINIA

The division of the sums of squares of the shortleaf pine in a form quite like the others is presented in Table 6. The bulk of the variation is due to slow change. As the data have been taken from stands of approximately even age, the trends representing slow change are ascribable both to advancing age and to changes in site quality. The effect of annual variation is relatively little, with 4 and 8 percent of the total sums of squares; it is, however, 22 and 23 percent of the more homogeneous portions.

The residuals from average trends of the shortleaf pine data of Figure 10 are listed in Table 7.

HEMLOCK IN NEW HAMPSHIRE

The hemlock data are subdivided according to the same classification as the others (Table 8). Slow change does not account for so high a portion of the sum of squares as in the pines. This may be due to the practical elimination of age as 7 of the 8 sections contained more than 200 annual rings. As with the oak data, it seems likely that the 28 percent of hemlock

TABLE 4. DIVISION OF LONGLEAF PINE SUMS OF SQUARES INTO PORTIONS DUE TO ASSIGNABLE CAUSES. LAKE CITY, GAINESVILLE, AND JACKSONVILLE, FLORIDA. UNITS OF HUNDREDTH MILLIMETERS SQUARED.

Due to	Lake City Data			Gainesville Data			Jacksonville Data		
	Degrees of freedom	Sum of squares	Percentages of total	Degrees of freedom	Sum of squares	Percentages of total	Degrees of freedom	Sum of squares	Percentages of total
Between tree means	11	1,236,703	3.8	17	2,949,549	17.2	11	446,522	4.7
Between years:									
Average trend (slow change)	4	21,890,219	67.5	6	7,468,548	43.7	3	3,519,464	36.9
Residuals from trend	23	930,663	2.9	35	775,437	4.5	38	1,125,567	11.8
Unaccounted-for remainder	297	8,383,395	25.8	697	5,914,056	34.6	451	4,447,257	46.6
Total	335	32,440,980	100.0	755	17,107,590	100.0	503	9,538,810	100.0

TABLE 5. RESIDUALS FROM THE AVERAGE TREE TREND OF EACH GROUP, ACCORDING TO YEAR OF ANNUAL RING GROWTH, IN UNITS OF 0.01 MM. LONGLEAF PINE IN FLORIDA

Year	Group			Year	Group		
	Lake City	Gainesville	Jacksonville		Lake City	Gainesville	Jacksonville
1894	.....	—52.76	37.08	1915	64.24	0.46	13.17
1895	.....	8.14	22.83	1916	—89.17	— 6.08	—20.33
1896	.....	79.87	— 7.42	1917	—57.96	27.78	27.25
1897	.....	65.19	—31.92	1918	—45.61	—11.72	—32.25
1898	.....	—45.41	19.83	1919	43.07	—65.04	100.50
1899	.....	—51.41	— 0.08	1920	18.07	—39.59	25.75
1900	.....	18.38	—55.75	1921	12.45	—37.53	—68.00
1901	.....	—20.96	19.67	1922	12.92	—27.17	— 8.75
1902	.....	—30.03	32.08	1923	—14.31	26.24	— 3.58
1903	.....	—27.06	16.08	1924	35.45	30.55	—12.58
1904	.....	— 4.42	—65.58	1925	—61.57	54.28	—40.50
1905	.....	32.99	—26.08	1926	16.12	35.72	— 9.92
1906	.....	— 2.52	—41.25	1927	— 0.41	23.88	—24.42
1907	.....	—11.76	—57.58	1928	70.20	15.88	39.75
1908	2.41	30.65	—16.92	1929	84.30	—23.32	46.25
1909	—60.05	17.02	—18.33	1930	—31.76	—21.42	—67.25
1910	—27.17	3.45	—54.92	1931	—60.48	—49.20	—79.50
1911	105.60	20.69	95.75	1932	—68.16	— 2.96	—34.67
1912	35.03	— 8.58	133.50	1933	— 2.82	4.44	19.75
1913	66.66	11.88	61.75	1934	— 2.85	10.16	35.09
1914	—87.35	12.85	—22.92	1935	43.09	8.44	54.42
General Mean					485.25	293.85	310.89

TABLE 6. DIVISION OF SHORTLEAF PINE SUMS OF SQUARES INTO PORTIONS DUE TO ASSIGNABLE CAUSES. "DEAD" AND "LIVE" TREE GROUPS, HERNDON, VIRGINIA. UNITS OF HUNDREDTH MILLIMETERS SQUARED.

Due to	"Dead" Tree Group			"Live" Tree Group		
	Degrees of freedom	Sum of squares	Percentages of total	Degrees of freedom	Sum of squares	Percentages of total
Between tree means	13	1,051,584	7.2	14	2,127,388	19.4
Between years:						
Average trend (slow change)	3	10,690,286	72.9	3	5,208,386	47.5
Residuals from trend	75	632,357	4.3	58	829,035	7.6
Unaccounted-for remainder	1,014	2,294,443	15.6	854	2,801,012	25.5
Total	1,105	14,668,670	100.0	929	10,965,821	100.0

sum of squares accounted for by the averaged trend, is ascribable to the longer time changes in site quality.

Residuals from average trends of the hemlock data of Figure 11 are given in Table 9.

TABLE 7. RESIDUALS FROM THE AVERAGE TREE TREND OF EACH GROUP ACCORDING TO YEAR OF ANNUAL GROWTH, IN UNITS OF 0.01 MM. SHORTLEAF PINE IN VIRGINIA

Year	"Dead" trees	"Live" trees	Year	"Dead" trees	"Live" trees	Year	"Dead" trees	"Live" trees
1854	64.64		1881	—16.64	—46.40	1908	—25.50	— 1.67
1855	73.43		1882	— 5.36	21.40	1909	—16.86	— 5.07
1856	3.29		1883	— 8.71	—27.13	1910	—18.00	4.53
1857	—66.57		1884	4.64	13.27	1911	—16.64	2.87
1858	—88.50		1885	7.29	—11.60	1912	2.86	30.73
1859	—14.00		1886	12.07	23.67	1913	21.57	45.87
1860	22.14		1887	6.50	—43.33	1914	0.21	— 3.20
1861	34.07		1888	— 3.57	—35.60	1915	— 5.71	0.27
1862	14.79		1889	7.57	40.73	1916	8.50	44.00
1863	— 0.43		1890	32.71	35.40	1917	0.64	— 4.93
1864	—31.57		1891	22.21	1.73	1918	—19.86	—18.60
1865	—16.64		1892	3.00	— 6.80	1919	—20.71	— 1.60
1866	— 2.79		1893	0.07	—31.60	1920	—24.57	—21.13
1867	33.64		1894	3.21	9.13	1921	—13.29	11.13
1868	— 2.93		1895	6.57	—12.13	1922	5.14	9.00
1869	—44.21		1896	6.00	12.73	1923	— 2.43	—16.67
1870	—26.64		1897	40.93	74.53	1924	4.29	1.40
1871	—23.64		1898	50.43	28.27	1925	10.79	20.47
1872	— 6.79		1899	28.57	14.33	1926	— 1.71	—22.53
1873	— 1.00		1900	10.64	— 0.67	1927	— 2.21	—14.60
1874	— 6.86	—43.40	1901	— 2.93	—35.60	1928	14.21	6.00
1875	—22.71	—45.27	1902	—15.29	—34.53	1929	17.43	26.60
1876	2.21	24.93	1903	—15.79	—20.93	1930	4.64	11.47
1877	10.50	47.60	1904	— 8.14	—19.60	1931	9.14	3.73
1878	28.86	118.10	1905	— 0.79	—17.33	1932	1.93	—28.13
1879	19.21	—20.07	1906	—19.57	—23.20	1933		—10.67
1880	— 4.71	—38.47	1907	—26.29	—29.50	1934		0.20
						1935		7.93

General mean "Dead" trees: 155.31
"Live" trees: 178.13

TABLE 8. DIVISION OF HEMLOCK SUMS OF SQUARES INTO PORTIONS DUE TO ASSIGNABLE CAUSES. HANOVER, NEW HAMPSHIRE. UNITS OF HUNDREDTH MILLIMETERS SQUARED.

Due to	Degrees of freedom	Sum of squares	Percent of total
Between tree means	7	953,490	19.6
Between years:			
Average trend (slow change)	10	1,349,871	27.7
Residuals from trend	89	600,516	12.3
Unaccounted-for remainder	693	1,967,245	40.4
Total	799	4,871,122	100.0

TRANSFORMATION OF SCALE

Had each locality been represented by only a single group, the investigation of the influence of precipitation upon the annual variation of tree ring width would have been performed upon the residuals from trends as meas-

TABLE 9. RESIDUAL FROM AVERAGE TREE TREND ACCORDING TO YEAR OF ANNUAL RING GROWTH, IN UNITS OF 0.01 MM. HEMLOCK AT HANOVER, NEW HAMPSHIRE

Year	Residual	Year	Residual	Year	Residual	Year	Residual
1835	31.99	1860	12.54	1885	—39.44	1910	38.69
1836	—30.48	1861	9.36	1886	7.20	1911	—26.23
1837	—16.26	1862	—18.57	1887	—28.66	1912	14.40
1838	33.85	1863	4.82	1888	—19.51	1913	— 2.04
1839	— 1.55	1864	—11.88	1889	13.44	1914	—31.97
1840	12.95	1865	—15.08	1890	46.45	1915	31.88
1841	—19.35	1866	8.85	1891	0.80	1916	71.75
1842	38.94	1867	24.80	1892	55.24	1917	— 5.14
1843	—34.58	1868	21.40	1893	19.80	1918	—39.70
1844	—14.67	1869	—30.15	1894	40.74	1919	19.37
1845	31.51	1870	— 4.92	1895	—45.67	1920	—49.93
1846	1.86	1871	— 1.68	1896	— 39.41	1921	23.85
1847	5.51	1872	—25.45	1897	— 1.70	1922	31.66
1848	5.35	1873	—21.22	1898	18.74	1923	—31.71
1849	15.46	1874	24.78	1899	—24.30	1924	—13.83
1850	— 0.10	1875	26.34	1900	—37.02	1925	—10.83
1851	26.38	1876	— 0.25	1901	— 3.12	1926	—17.30
1852	—32.42	1877	—22.42	1902	44.96	1927	13.77
1853	—38.88	1878	21.13	1903	51.02	1928	— 7.64
1854	—36.69	1879	—10.78	1904	—29.87	1929	22.79
1855	—22.12	1880	34.42	1905	—22.66	1930	48.91
1856	3.56	1881	3.05	1906	2.70	1931	—27.05
1857	30.24	1882	20.17	1907	—36.25	1932	—17.95
1858	67.81	1883	—41.66	1908	—24.48	1933	— 6.57
1859	—21.37	1884	—14.88	1909	13.01	1934	8.45

General mean: 150.85

ured in absolute units, that is, as listed in Tables 3, 5, 7, and 9. As it happens, however, each locality, except Hanover (the hemlock data), is represented by more than one group. Interest, therefore, is centered not only on the average influence of precipitation upon the species according to the grouping, but also on the possibility of its differential influence upon the groups within each locality.

One hesitates, however, to pool the annual variations of the groups within localities, when annual variation is measured in absolute units, because in some cases they differ radically, as is brought out in Table 10. The pertinent columns of this table are those which list the standard deviations of the average ring width residuals, and their coefficients of variation. How the standard deviations are derived may be illustrated in the case of trees numbered 1 to 12 of the oak in North Carolina: The mean square of residuals from trend (column 1) is, of course, the sum of squares between years—108,518 from table 2—divided by the degrees of freedom upon which it is based—29, also from Table 2. But this mean square is 12 times the variance between years since it is based upon 12 trees. Its division by 12, then, gives the variance of the annual ring widths, and these are listed in column 3 of Table 10. The standard deviation (column 4) is the square root of the variance.

In two localities of the three which are represented by more than one

TABLE 10. COMPARISON OF ABSOLUTE AND RELATIVE MEASURES OF ANNUAL RING WIDTH VARIATION

Locality and group	Mean square of residuals from trend	Number of trees	Variance between years	Standard deviation	General mean	Coefficient of variation
	(0.01 mm)²		*(0.01 mm)²*	*(0.01 mm)*	*(0.01 mm)*	*Percent*
Oak in North Carolina:						
Trees 1 to 12	3,742.0	12	311.83	17.7	171.0	10.4
Trees 13 to 17	311.3	5	62.26	7.9	91.4	8.6
Longleaf pine in Florida:						
At Lake City	40,463.6	12	3,371.97	58.1	485.3	12.0
At Gainesville	22,155.3	18	1,230.85	35.1	293.9	11.9
At Jacksonville	29,620.2	12	2,468.35	49.7	310.9	16.0
Shortleaf pine in Virginia:						
"Dead" trees	8,431.4	14	602.24	24.5	155.3	15.8
"Live" trees	14,293.7	15	952.91	30.9	178.1	17.3
Hemlock in New Hampshire:	6,747.4	8	843.42	29.0	150.8	19.2

group, there is very considerable variation among the standard deviations. On the other hand, the coefficients of variation, that is, the ratios of the standard deviations to corresponding means, are fairly uniform within their respective localities (column 6). This suggests that the groups within localities may be pooled and considered, for the present at least, as parts of common locality populations, provided the residuals be measured on a relative scale. Should differential influence of precipitation upon groups within localities be then discovered, it would not have been due to the circumstance that different groups have different general means.

Henceforth then, average annual variation will be measured in terms of the logarithmic transformation of the observations of Tables 3, 5, and 7; that is,

$$\log_{10} \frac{\text{General mean} + \text{residual}}{\text{General mean}}$$

in which a residual is taken from Table 3, 5, or 7, according to year and group, and the general mean is that of the same group as given at the bottom of the table.

Expressed in this form the residuals should supply homogeneous material for the study of precipitation effects between and within groups of the same species. It was decided, therefore, to base subsequent analyses of the oak and pine on the logarithmic scale. There is no advantage, however, in the transformation of the hemlock residuals; for these fall into a single group. They alone are maintained in the original absolute scale.

METHOD OF INVESTIGATING INFLUENCE OF PRECIPITATION

The present investigation of the influence of precipitation on the annual variation of tree ring width is based upon the method employed by Schu-

macher and Meyer (1937) on white fir in Switzerland. The method is essentially that developed by Fisher (1925) in dealing with rainfall-wheat yield relationships in England. In brief outline it is as follows:

If the average effect of an additional inch of precipitation during a short time interval (t) within a given period of time on the width of annual rings (on any scale) may be expressed by the equation

$$w = a_0 + a_1\left[X_1(t)\right] + a_2\left[X_2(t)\right] + \ldots\ldots + a_k\left[X_k(t)\right] \ldots\ldots (2)$$

in which $X_1(t)$, $X_2(t)$, . . . , $X_k(t)$ are orthogonal functions of the time interval (t) during the period, and a_0, a_1, a_2 . . . a_k are constants to be determined; and if the precipitation within the same time interval (t) of the same period may be expressed

$$p = \alpha_0 + \alpha_1\left[X_1(t)\right] + \alpha_2\left[X_2(t)\right] + \ldots\ldots + \alpha_k\left[X_k(t)\right] \ldots\ldots (3)$$

then the whole effect of the precipitation distribution during the period on the width (w) of an annual ring may be written

$$(w - M_w) = \sum_{t=-\frac{T}{2}}^{t=\frac{T}{2}} (w \cdot p) \ldots\ldots\ldots\ldots (4)$$

where M_w is the mean value of the observed annual ring widths. The summation is carried over all time intervals of the period, the first and last of which are denoted by $-\frac{T}{2}$ and $\frac{T}{2}$ respectively, T being the number of time intervals within the period. On account of certain properties of the orthogonal functions $X_i(t)$, $[i = 0, 1, 2, \ldots k]$, such as

$$\sum_{t=-\frac{T}{2}}^{t=\frac{T}{2}} (X_i) = 0; \quad \sum_{t=-\frac{T}{2}}^{t=\frac{T}{2}} (X_i^2) = T; \text{ and } \sum_{t=-\frac{T}{2}}^{t=\frac{T}{2}} (X_i X_j) = 0;$$

where i differs from j, $[j = 0, 1, 2, \ldots k]$, upon substituting (2) and (3) into (4), the latter becomes

$$w - M_w = T(a_0\alpha_0 + a_1\alpha_1 + a_2\alpha_2 + \ldots\ldots + a_k\alpha_k) \ldots\ldots (5)$$

The object of the analysis is the pictorial representation of equation (2). The coefficients α_0, α_1, . . . , α_k of equation (3) are first determined by the method of least squares from the rainfall record of each period at the Weather Bureau stations. These coefficients are then regarded as $(k + 1)$ independ-

ent variates, in terms of which the annual ring width residuals $(w - M_w)$ are to be expressed according to the method of least squares. The solution affords estimates of the unknowns $a_0, a_1, \ldots, a_k$. Finally, upon putting these in equation (2) the average effect appears of an additional inch of precipitation in each time interval of the period on the width of annual ring.

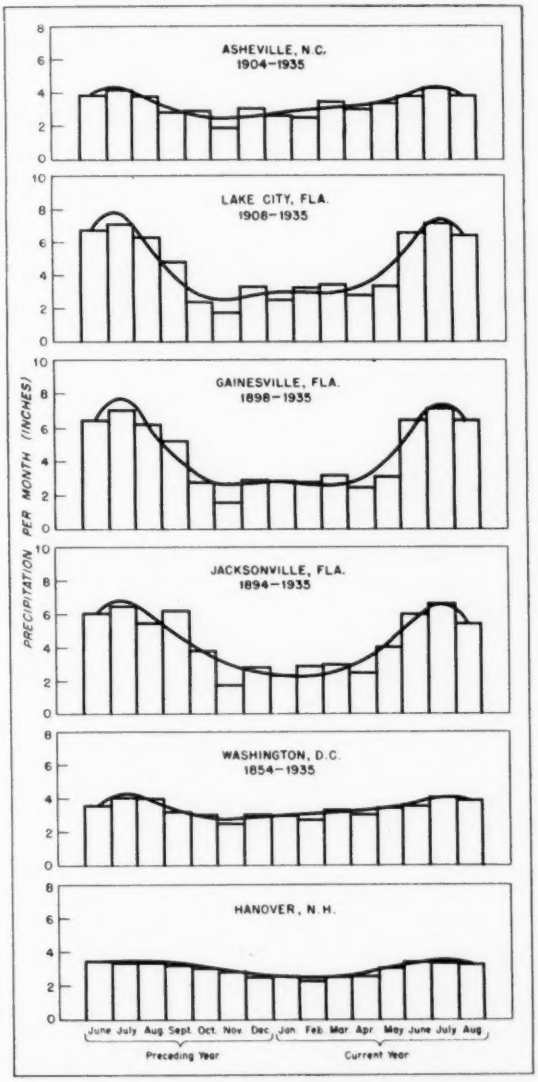

FIG. 12. Comparison of the average precipitation trends with the recorded average monthly precipitation over the 15-month periods at the U. S. Weather Bureau stations.

Period lengths of 15 months were chosen beginning with June 1 of the year preceding growth of the annual ring, and ending with August 31 of the year of growth. The precipitation records used are by months, hence the time interval t is 1 month, and T, the number of intervals in the period, is 15.

THE PRECIPITATION DISTRIBUTION CONSTANTS

The first part of the work is the determination of the precipitation coefficients $a_0, a_1, \ldots, a_k$ of the orthogonal polynomial equation (3) which describes the precipitation distribution of each period for which data are at hand. Polynomials of degree 6 were chosen. Calculation of the coefficients is facilitated through the use of published tables of orthogonal functions. A very convenient set is given by Lorenz (1931) together with a full discussion of the theory, and application to specific problems.

Employing the computational scheme and checking method as recommended by Lorenz, precipitation coefficients were calculated for each of the

TABLE 11. COEFFICIENTS OF ORTHOGONAL POLYNOMIALS WHICH EXPRESS PRECIPITATION TRENDS (IN HUNDREDTHS OF INCHES) AT ASHEVILLE, N. C., BY MONTHLY INTERVALS FROM JUNE OF A PRECEDING YEAR TO AUGUST, INCLUSIVE, OF A CURRENT YEAR, FOR THE CURRENT YEARS 1904 TO 1935

Current year	COEFFICIENTS						
	a_0	a_1	a_2	a_3	a_4	a_5	a_6
1904	285	— 20	98	— 66	3	25	— 15
1905	355	115	103	— 30	— 30	— 60	— 92
1906	401	— 21	78	— 31	— 28	52	—190
1907	323	— 81	91	— 29	— 44	— 5	72
1908	350	84	73	57	50	20	— 27
1909	463	54	46	— 1	—163	56	— 31
1910	387	20	212	6	30	3	2
1911	354	— 20	149	27	21	138	35
1912	331	4	— 3	6	—107	44	— 13
1913	302	6	34	— 76	— 27	33	14
1914	279	38	81	30	— 16	12	11
1915	388	— 41	24	35	16	— 63	2
1916	377	31	69	11	— 41	—103	— 80
1917	348	— 32	115	— 50	4	70	— 69
1918	341	23	89	— 24	— 41	24	4
1919	412	— 83	— 8	11	— 14	— 91	46
1920	299	79	89	— 40	63	80	19
1921	360	— 2	17	19	— 54	10	— 80
1922	318	— 10	35	— 82	— 5	14	— 51
1923	313	32	27	— 63	— 4	0	— 22
1924	290	17	27	— 29	— 14	15	— 72
1925	229	— 70	— 18	— 26	— 33	46	— 42
1926	230	71	10	19	40	— 24	0
1927	276	15	30	0	— 28	5	— 71
1928	388	90	98	16	45	9	51
1929	372	— 64	20	— 62	—118	69	16
1930	267	— 88	25	40	— 57	— 44	97
1931	257	35	20	— 2	2	1	59
1932	266	— 7	— 24	— 43	45	11	— 66
1933	322	26	4	37	8	— 47	34
1934	289	24	40	— 69	— 58	17	— 42
1935	359	— 13	45	— 17	17	— 48	— 17
Average	329.09	6.62	53.00	— 13.31	— 16.81	8.41	— 16.19

15-month periods ending with August 31, according to the years and localities represented by the annual ring data. These are as follows: 1904 to 1935 at Asheville, North Carolina (Table 11); 1908 to 1935 at Lake City, Florida (Table 12); 1898 to 1935 at Gainesville, Florida (Table 13); 1894 to 1935 at Jacksonville, Florida (Table 14); 1854 to 1935 at Washington, D. C. (Table 15); 1836 to 1934 (omitting 1856 to 1867 for which there were no records) at Hanover, New Hampshire (Table 16).

At the bottom of each table is the average of each coefficient. From these the precipitation trends for the average period over the years listed have been calculated, and they are compared with the recorded average rainfall in Figure 12.

TABLE 12. COEFFICIENTS OF ORTHOGONAL POLYNOMIALS WHICH EXPRESS PRECIPITATION TRENDS (IN HUNDREDTHS OF INCHES) AT LAKE CITY, FLA., BY MONTHLY INTERVALS FROM JUNE OF A PRECEDING YEAR TO AUGUST, INCLUSIVE, OF A CURRENT YEAR, FOR THE CURRENT YEARS 1908 TO 1935

Current year	COEFFICIENTS						
	α_0	α_1	α_2	α_3	α_4	α_5	α_6
1908	391	—117	100	— 14	— 25	— 5	— 66
1909	402	190	217	6	— 88	— 56	—132
1910	522	17	368	— 12	— 65	48	—204
1911	476	— 61	417	9	39	28	1
1912	580	— 20	87	38	—116	63	— 47
1913	515	— 82	181	64	— 15	— 29	— 29
1914	449	— 38	100	34	34	64	—171
1915	470	— 19	79	37	— 38	— 6	— 80
1916	420	— 51	134	31	—135	—105	— 24
1917	438	— 27	124	26	66	— 63	— 85
1918	401	44	131	— 30	— 66	76	— 37
1919	554	66	151	33	— 9	— 32	— 57
1920	521	— 47	168	— 69	— 39	120	— 12
1921	446	— 49	99	93	—135	— 66	— 29
1922	425	— 1	98	— 47	— 58	— 8	— 68
1923	422	31	125	— 38	— 63	— 21	10
1924	438	8	98	—152	0	1	— 61
1925	436	— 34	153	— 17	— 72	— 60	— 38
1926	505	77	210	— 46	22	— 92	—112
1927	480	— 79	232	— 43	— 69	27	—113
1928	559	99	166	—198	43	67	70
1929	505	— 46	180	— 12	— 51	34	7
1930	458	— 58	49	— 54	— 39	62	— 73
1931	456	36	125	— 24	— 7	— 67	— 75
1932	396	47	213	— 41	— 73	113	—116
1933	525	— 9	163	— 9	36	76	65
1934	482	49	159	— 1	—219	25	— 75
1935	451	69	361	10	29	9	—146
Average	468.68	— 0.18	167.43	— 15.21	— 39.75	7.25	— 60.61

TABLE 13. COEFFICIENTS OF ORTHOGONAL POLYNOMIALS WHICH EXPRESS PRECIPITATION TRENDS (IN HUNDREDTHS OF INCHES) AT GAINESVILLE, FLA., BY MONTHLY INTERVALS FROM JUNE OF A PRECEDING YEAR TO AUGUST, INCLUSIVE, OF A CURRENT YEAR, FOR THE CURRENT YEARS 1898 TO 1935

Current year	COEFFICIENTS						
	α_0	α_1	α_2	α_3	α_4	α_5	α_6
1898	461	30	203	122	— 63	— 12	— 96
1899	469	— 87	149	125	— 29	104	—151
1900	444	44	34	—114	—168	103	— 36
1901	501	95	169	— 75	133	— 15	— 57
1902	421	—114	174	— 60	— 92	15	— 66
1903	558	— 7	77	48	77	— 35	12
1904	420	— 29	107	1	— 5	18	—180
1905	500	131	294	96	9	24	— 14
1906	573	— 71	243	— 8	—195	— 45	—131
1907	370	— 70	295	— 89	— 30	4	— 51
1908	446	— 35	123	87	—105	— 43	— 65
1909	456	— 7	274	29	— 92	—104	—122
1910	462	27	288	— 1	— 83	84	—217
1911	419	—134	268	12	20	1	60
1912	493	88	78	60	— 73	— 6	— 56
1913	539	— 74	225	17	25	— 6	— 20
1914	440	— 97	77	47	— 54	41	—182
1915	398	— 44	79	34	— 5	18	— 37
1916	423	26	155	104	— 80	—103	25
1917	410	— 81	142	64	9	0	—100
1918	379	49	178	80	— 48	121	7
1919	505	31	122	65	— 74	34	— 18
1920	531	— 15	136	— 55	— 77	45	6
1921	476	— 26	180	72	—146	—143	—151
1922	488	— 66	155	— 19	— 43	58	— 73
1923	451	49	120	27	—143	— 39	56
1924	507	43	170	—169	41	— 68	—105
1925	456	— 83	210	43	— 62	36	—151
1926	494	40	110	2	— 5	9	—131
1927	441	— 58	201	— 17	— 46	— 35	— 70
1928	509	124	296	— 77	30	15	30
1929	536	— 93	189	— 16	—132	105	— 58
1930	489	— 23	84	— 88	—101	— 3	— 19
1931	474	— 24	184	— 25	94	— 65	— 3
1932	344	22	145	— 31	—127	112	—143
1933	442	3	158	— 64	68	21	77
1934	455	60	99	— 1	—214	74	12
1935	452	84	324	58	21	— 33	— 34
Average	464.00	— 7.68	171.45	7.47	— 46.45	7.55	— 59.26

TABLE 14. COEFFICIENTS OF ORTHOGONAL POLYNOMIALS WHICH EXPRESS PRECIPITATION TRENDS (IN HUNDREDTHS OF INCHES) AT JACKSONVILLE, FLA., BY MONTHLY INTERVALS FROM JUNE OF A PRECEDING YEAR TO AUGUST, INCLUSIVE, OF A CURRENT YEAR, FOR THE CURRENT YEARS 1894 TO 1935

Current year	Coefficients						
	α_0	α_1	α_2	α_3	α_4	α_5	α_6
1894	447	— 7	168	135	— 38	45	— 32
1895	553	—100	95	88	—202	3	— 49
1896	377	— 21	191	0	— 53	18	—111
1897	426	— 45	123	— 42	69	5	15
1898	480	— 58	132	181	—130	— 67	24
1899	435	— 74	72	66	— 78	39	—143
1900	415	21	34	—126	—100	61	7
1901	488	37	81	— 65	27	— 59	38
1902	391	— 68	181	— 33	— 10	— 1	4
1903	565	— 32	0	66	—101	30	110
1904	339	— 8	24	34	— 32	— 41	— 76
1905	501	41	103	106	18	41	128
1906	502	50	105	32	—185	7	— 47
1907	344	3	202	— 20	— 83	86	— 13
1908	415	— 19	83	72	—141	— 21	— 85
1909	511	— 69	175	110	—234	4	16
1910	385	— 55	243	— 37	— 26	— 4	— 78
1911	366	— 54	210	106	14	37	85
1912	462	76	51	22	— 93	— 23	— 48
1913	434	—109	141	— 46	— 8	2	— 37
1914	340	5	136	65	84	64	— 79
1915	406	— 18	48	125	— 80	1	—121
1916	373	— 37	143	134	—131	23	— 20
1917	425	— 19	161	114	— 9	— 90	— 54
1918	332	— 66	113	— 39	—101	130	— 79
1919	468	145	104	8	—126	— 91	14
1920	556	— 41	228	—122	25	— 21	11
1921	439	— 36	231	77	— 21	— 52	— 40
1922	471	7	107	33	— 72	108	— 52
1923	434	— 46	117	46	—136	— 46	84
1924	428	35	101	— 5	— 43	— 17	—115
1925	452	— 87	155	74	—127	25	— 34
1926	454	46	106	— 23	— 57	—117	—155
1927	415	—152	200	— 22	— 84	— 68	— 92
1928	417	57	163	— 98	12	19	— 29
1929	463	— 2	158	22	—134	65	— 33
1930	448	— 32	48	— 97	—163	57	— 76
1931	370	— 37	110	—115	82	— 19	69
1932	413	230	137	—108	—203	—144	— 77
1933	604	—150	352	—227	78	—181	58
1934	533	— 14	187	— 24	—164	— 52	17
1935	453	— 11	314	— 41	50	— 58	19
Average	441.19	— 17.00	138.88	10.14	— 64.43	— 7.19	— 25.62

TABLE 15. COEFFICIENTS OF ORTHOGONAL POLYNOMIALS WHICH EXPRESS PRECIPITATION TRENDS (IN HUNDREDTHS OF INCHES) AT WASHINGTON, D. C., BY MONTHLY INTERVALS FROM JUNE OF A PRECEDING YEAR TO AUGUST, INCLUSIVE, OF A CURRENT YEAR, FOR THE CURRENT YEARS 1854 TO 1935

Current year	COEFFICIENTS						
	α_0	α_1	α_2	α_3	α_4	α_5	α_6
1854	276	— 40	— 55	— 23	— 35	51	7
1855	217	49	29	24	— 38	— 71	— 17
1856	322	2	87	— 33	— 21	— 50	— 1
1857	345	80	190	6	6	— 11	41
1858	368	— 46	102	— 23	— 44	23	— 6
1859	350	0	— 50	— 2	— 14	28	— 26
1860	320	2	40	11	3	— 18	74
1861	368	66	61	74	— 17	19	23
1862	390	— 24	35	— 29	— 73	33	— 35
1863	351	13	23	— 86	— 12	2	— 74
1864	331	— 10	0	— 25	— 15	103	42
1865	353	112	— 40	— 45	— 82	— 30	— 50
1866	365	— 18	64	— 42	5	— 45	—132
1867	528	57	72	76	10	101	92
1868	438	— 33	100	23	— 68	— 12	15
1869	383	— 86	— 8	— 47	— 33	2	— 28
1870	349	22	— 32	— 24	— 10	— 71	25
1871	310	20	54	— 58	— 41	— 38	— 34
1872	280	— 33	116	36	48	39	40
1873	381	40	21	71	3	45	50
1874	317	— 51	— 4	18	—116	40	33
1875	333	86	140	134	105	94	77
1876	396	— 9	37	44	— 92	78	— 56
1877	417	— 36	68	18	—118	— 21	11
1878	539	55	114	65	10	— 67	0
1879	431	—109	143	82	10	50	— 38
1880	325	0	27	— 34	— 18	81	— 15
1881	333	— 15	— 64	— 51	10	3	— 31
1882	381	38	— 25	— 36	121	— 46	— 23
1883	387	38	33	— 17	—100	26	— 45
1884	451	— 15	41	—138	15	— 47	— 94
1885	356	— 17	102	— 31	129	2	— 75
1886	523	99	— 4	— 40	—131	— 83	— 28
1887	354	— 95	94	— 94	21	47	— 93
1888	323	41	10	— 25	0	— 2	— 29
1889	496	95	9	— 87	—133	— 11	49
1890	390	— 52	83	10	— 3	49	22
1891	453	77	— 19	6	— 31	32	— 70
1892	394	— 53	12	— 98	— 28	64	— 97
1893	271	— 7	— 6	— 45	— 3	35	— 1
1894	271	— 9	— 53	26	— 10	— 15	46
1895	289	63	— 43	— 39	— 39	— 29	— 22
1896	277	3	27	— 63	54	26	— 57
1897	319	75	32	— 57	— 39	38	— 28
1898	334	26	86	82	58	68	— 3
1899	371	18	— 18	45	— 10	55	— 98
1900	368	0	25	— 39	—127	10	— 22
1901	363	— 9	135	—106	46	— 85	81
1902	348	— 41	— 15	— 58	41	8	— 85
1903	430	27	— 45	30	39	— 27	22
1904	325	22	85	— 26	— 62	— 16	— 63
1905	450	83	188	58	23	— 4	— 61
1906	514	53	251	115	24	152	— 97
1907	435	—119	105	— 5	—100	99	— 5
1908	374	— 16	20	42	18	— 11	55
1909	305	— 7	— 20	— 16	— 54	64	— 7

TABLE 15. *(Continued)*

Current year	COEFFICIENTS						
	α_0	α_1	α_2	α_3	α_4	α_5	α_6
1910.....	284	30	4	— 72	— 28	— 36	— 9
1911.....	332	37	101	51	55	— 33	14
1912.....	410	— 15	29	— 38	— 72	— 23	— 58
1913.....	367	— 1	67	— 37	6	84	16
1914.....	334	39	35	48	— 13	39	— 18
1915.....	362	23	95	12	80	— 24	— 60
1916.....	356	— 12	105	— 56	— 54	— 40	— 26
1917.....	373	— 2	100	— 97	— 24	—105	—110
1918.....	343	— 62	69	—115	7	49	— 29
1919.....	331	87	22	— 34	— 24	— 7	— 58
1920.....	361	17	78	0	— 16	17	— 69
1921.....	344	— 35	45	— 67	— 58	— 16	— 47
1922.....	369	71	47	— 22	— 7	— 62	—116
1923.....	365	— 74	62	— 34	— 39	70	— 97
1924.....	370	72	14	— 70	— 12	81	28
1925.....	299	— 49	57	55	— 16	22	— 5
1926.....	306	6	31	94	11	26	— 26
1927.....	356	— 47	— 5	82	— 76	26	49
1928.....	384	117	133	120	122	74	116
1929.....	359	— 59	20	— 25	—175	100	5
1930.....	272	— 72	25	— 56	19	—86	66
1931.....	243	103	84	— 37	36	24	15
1932.....	312	— 13	— 22	— 58	— 51	84	— 40
1933.....	461	123	46	110	29	— 52	85
1934.....	370	— 58	99	11	— 57	128	— 36
1935.....	415	— 97	— 36	84	—118	33	86
Average....	362.76	6.60	44.70	— 7.28	— 16.99	13.78	— 14.21

TABLE 16. COEFFICIENTS OF ORTHOGONAL POLYNOMIALS WHICH EXPRESS PRECIPITATION TRENDS (IN HUNDREDTHS OF INCHES) AT HANOVER, NEW HAMPSHIRE, BY MONTHLY INTERVALS FROM JUNE OF A PRECEDING YEAR TO AUGUST, INCLUSIVE, OF A CURRENT YEAR, FOR THE CURRENT YEARS 1836 TO 1855 AND 1868 TO 1934

Current year	Coefficients						
	α_0	α_1	α_2	α_3	α_4	α_5	α_6
1836	303	— 30	3	— 60	21	16	— 22
1837	309	43	— 11	— 31	— 15	— 64	— 8
1838	296	33	73	— 36	— 31	— 30	5
1839	322	— 56	75	— 10	— 19	—115	21
1840	336	— 9	14	— 89	20	11	7
1841	357	— 40	— 57	19	6	— 6	26
1842	326	67	31	16	12	15	0
1843	464	50	44	64	3	73	38
1844	432	— 36	80	72	— 4	— 20	26
1845	373	— 87	— 17	37	13	46	3
1846	297	22	— 34	8	— 46	— 47	— 6
1847	357	22	25	1	30	— 33	— 4
1848	401	18	66	36	— 12	— 23	2
1849	370	— 7	99	135	0	71	29
1850	369	— 9	26	15	—114	— 19	60
1851	370	— 20	— 68	— 27	51	— 18	— 96
1852	336	— 12	— 15	33	— 20	— 61	10
1853	301	— 27	27	— 33	20	— 4	32
1854	289	— 33	— 76	0	— 65	— 29	45
1855	293	45	40	19	— 3	—103	7
1868	290	30	52	— 32	— 50	— 17	74
1869	308	— 19	51	— 18	— 14	7	71
1870	339	— 81	— 51	36	— 40	— 24	50
1871	193	7	48	1	5	— 7	66
1872	269	106	109	68	3	— 25	— 13
1873	298	— 73	82	— 10	— 46	37	—104
1874	301	— 9	28	25	— 75	— 31	— 29
1875	288	12	81	— 5	— 20	9	— 21
1876	261	— 57	31	— 44	— 25	— 20	— 17
1877	308	66	75	17	11	— 69	— 89
1878	291	— 95	89	3	— 37	9	— 50
1879	276	10	10	2	45	— 22	— 34
1880	255	— 48	40	35	19	— 22	3
1881	225	— 4	6	1	— 55	— 39	— 31
1882	235	— 14	19	— 19	1	— 59	— 19
1883	220	— 19	44	— 8	— 63	— 32	— 11
1884	253	10	29	— 14	16	33	6
1885	261	54	75	67	78	23	— 1
1886	294	— 66	— 2	71	— 30	2	— 3
1887	340	50	— 34	14	34	— 28	— 67
1888	329	16	28	— 23	16	54	— 46
1889	337	— 54	21	48	— 34	— 84	— 6
1890	375	29	76	62	31	10	28
1891	347	— 46	28	61	— 58	20	— 42
1892	320	62	97	— 13	— 22	— 7	— 7
1893	330	— 14	104	— 49	33	8	11
1894	263	— 57	46	— 12	— 10	— 8	1
1895	249	13	16	24	— 17	— 1	34
1896	298	2	— 20	0	32	30	— 15
1897	350	56	44	— 16	—130	— 66	— 15
1898	348	— 59	45	— 36	64	4	— 62
1899	296	— 20	26	24	— 10	— 39	16
1900	293	— 25	15	— 20	13	42	— 31
1901	295	43	18	1	— 28	— 28	29

TABLE 16. *(Continued)*

Current year	COEFFICIENTS						
	α_0	α_1	α_2	α_3	α_4	α_5	α_6
1902	308	31	28	— 12	— 59	49	— 23
1903	353	— 1	39	24	— 11	— 23	— 44
1904	285	— 42	88	— 51	28	25	7
1905	294	55	74	56	— 90	— 19	— 24
1906	339	— 52	96	— 48	— 86	17	— 4
1907	252	— 16	20	— 51	— 42	— 19	14
1908	293	— 34	2	33	— 8	— 48	70
1909	243	19	— 12	— 21	30	43	— 8
1910	248	23	19	3	5	8	37
1911	290	46	73	25	— 17	— 47	— 63
1912	330	— 53	62	— 15	— 54	70	5
1913	289	— 3	— 50	32	— 45	32	20
1914	278	36	— 28	9	2	46	22
1915	276	87	92	53	4	— 33	—126
1916	352	— 29	66	— 37	— 72	64	—106
1917	296	— 22	83	— 23	— 22	— 25	25
1918	284	— 15	86	— 27	27	— 34	71
1919	297	— 23	40	18	— 38	18	85
1920	341	19	— 37	16	— 43	31	58
1921	311	— 34	— 19	42	— 13	14	26
1922	336	67	13	— 17	— 34	— 23	21
1923	293	— 66	69	— 94	13	— 9	26
1924	312	14	— 30	55	— 4	— 2	37
1925	311	19	38	20	—110	— 36	— 30
1926	339	— 49	99	16	14	— 5	— 12
1927	280	— 54	37	45	— 42	— 6	— 17
1928	335	18	— 2	95	— 14	— 52	36
1929	275	— 14	41	— 49	— 47	38	22
1930	247	9	58	15	— 28	— 26	2
1931	301	61	88	— 31	— 84	— 61	— 63
1932	336	— 79	87	0	37	38	— 33
1933	336	28	14	12	— 36	38	64
1934	305	— 36	32	— 46	— 24	— 45	30
Average	308.06	— 4.02	33.53	5.25	— 15.85	— 7.61	— 0.28

REGRESSION OF GROWTH ON PRECIPITATION AT DIFFERENT SEASONS

The unknowns $a_0, a_1, \ldots, a_6$, of equation (5) were next calculated by the method of least squares, the dependent variate of each set being the transformed residual from average trend according to year, for the group under consideration. This variate, designated by (y) is the $(w - M_w)$ of equation (5).

WHITE OAK IN NORTH CAROLINA

As a step toward the solution of the normal equations for the white oak groups, the sums of squares and products of the independent variates—which are common to both groups—are found by correcting the crude sums of squares and products among the precipitation coefficients, $\alpha_0, \alpha_1, \ldots, \alpha_6$, for Asheville, to their respective means. The corrected values are given in Table 17.

Finally, there is needed to complete the normal equations, the sum of products of the dependent variate, y, with each independent variate in turn. The two groups, however, have been subjected to precisely the same precipitation distributions. Should they have reacted to them in perceptibly different ways, the regression of corresponding annual differences between groups on the precipitation coefficients would turn up as a significant departure from zero. In other words, if y_1 and y_2 denote the dependent variates of the first and second groups respectively, the regression equation

$$(Y_1 - Y_2) = a_0\alpha_0 + a_1\alpha_1 + \ldots\ldots + a_6\alpha_6 \ldots\ldots\ldots\ldots\ldots\ldots (5a)$$

in which $(Y_1 - Y_2)$ is the calculated value corresponding to the observed $(y_1 - y_2)$, should be significant. Should, however, such regression be an insignificant departure from zero, any differential response of the two groups to the same precipitation is not recognized, and therefore the best estimate

TABLE 17. CORRECTED SUMS OF SQUARES AND PRODUCTS OF THE RAINFALL COEFFICIENTS. ASHEVILLE, N. C., 1904 TO 1935

	α_0	α_1	α_2	α_3	α_4	α_5	α_6
α_0	93,875	2,360	29,431	11,215	—23,593	— 5,010	—14,487
α_1	.....	83,034	20,049	7,683	21,217	— 180	—17,150
α_2	.....	.....	81,016	1,836	20,000	21,622	1,301
α_3	.....	.....	.....	45,161	8,079	—17,917	19,680
α_4	.....	.....	.....	.....	76,797	— 7,292	8,408
α_5	.....	.....	.....	.....	.....	80,126	— 7,194
α_6	.....	.....	.....	.....	.....	.....	103,437

of the effect of precipitation on the oak data should be contained in the regression of the combined annual dependent variates of the two groups upon the precipitation coefficients; that is

$$(Y_1 + Y_2) = a_0\alpha_0 + a_1\alpha_1 + \ldots\ldots + a_6\alpha_6 \ldots\ldots\ldots\ldots\ldots\ldots (5b)$$

As another possible alternative, should both (5a) and (5b) turn up significant, the separate regressions for Y_1 and Y_2 may be obtained by taking half the sum and difference, respectively, of equations (5a) and (5b).

The sums of products of $(y_1 - y_2)$ and of $(y_1 + y_2)$ with each independent variate are given in Table 18.

Tests of significance of the regressions are based upon analyses of variance (Fisher, 1936). In general

$$S(y - M_y)^2 = S(y - Y)^2 + S(Y - M_y)^2$$

in which Y is the estimate of y by the method of least squares. The left-hand member of the above identity is the total sum of squares before eliminating that part due to regression on the precipitation distribution during the

15-month periods. The sum of squares due to the regression is calculated through the identity

$$S(Y-M_y)^2 = Ta_0 \cdot S\left[\alpha_0(y-M_y)\right] + Ta_1 \cdot S\left[\alpha_1(y-M_y)\right] + \ldots + Ta_6 \cdot S\left[\alpha_6(y-M_y)\right]$$

for which the sums of products are listed in Table 18 and the corresponding regression coefficients in Table 19. The remaining sum of squares, $S(y-Y)^2$, is due to deviation from regression; that is, it is that part of the total sum of squares that has been found to be independent of the precipitation distribution.

Sums of squares ascribable to these sources of variation are recorded for $(y_1 - y_2)$ and for $(y_1 + y_2)$, in turn, in Table 20, on the lines designated "Total," "Deviation from regression," and "Regression on $\alpha_0 \ldots \alpha_6$," respectively. It is useful to subdivide, for each regression, the sum of squares due to the last-named source—regression on precipitation coefficients—into two components, namely, (1) that which is ascribable to variation of total, or average, precipitation between the 15-month periods, dependent on α_0 only; and (2) the remaining component ascribable to variation in precipitation from season to season within the 15-month periods, dependent on the $\alpha_1 \ldots \alpha_6$ variation.

How the subdivision is carried out may be illustrated with the data $(y_1 - y_2)$. Had α_0—the average monthly precipitation of each period—been the only independent variate available, the regression of $(y - M_y)$ on α_0 would have been given by

$$\frac{S\left[\alpha_0(y-M_y)\right]}{S(\alpha_0 - M\alpha_0)^2} = \frac{1272}{93{,}875} = +0.013550$$

an effect that differs in sign from that given in Table 18—that is, —0.018037—which is the effect of α_0 independent of the other precipitation variates $\alpha_1 \ldots \alpha_6$. The sum of squares due to the use of α_0 alone is

$$\frac{\left\{S\left[\alpha_0(y-M_y)\right]\right\}^2}{S(\alpha_0 - M\alpha_0)^2} = \frac{(1272)^2}{93{,}875} = 17.2$$

Upon subtracting this quantity from the sum of squares due to $\alpha_0 \ldots \alpha_6$, the remainder, 908.7, is due to $\alpha_1 \ldots \alpha_6$; that is, to the differential effect of precipitation falling at different seasons of the period.

In an analogous manner the sum of squares of $(y_1 + y_2)$ are subdivided in the same table.

The total sum of squares in Table 20 is based upon 29 degrees of freedom among the 32 observations of sums and differences, since 2 degrees of

TABLE 18. CORRECTED SUMS OF PRODUCTS OF SUMS AND DIFFERENCES OF LOGARITHMIC RESIDUALS (X 10^5) AND THE PRECIPITATION COEFFICIENTS. WHITE OAK AT ASHEVILLE, N. C.

Group combination	Sum of Products With Rainfall Coefficient						
	α_0	α_1	α_2	α_3	α_4	α_5	α_6
$(y_1 - y_2)$..	1,272	2,991	— 4,216	716	259	—14,003	—12,425
$(y_1 + y_2)$..	55,384	12,053	1,574	—38,294	— 9,819	—23,379	—41,471

TABLE 19. REGRESSION COEFFICIENTS OF LOGARITHMIC RESIDUALS (X 10^5) ON THE RAINFALL COEFFICIENTS. WHITE OAK AT ASHEVILLE, N. C.

Group combination	$15a_0$	$15a_1$	$15a_2$	$15a_3$	$15a_4$	$15a_5$	$15a_6$
$(y_1 - y_2)$....	—0.018037	+0.005528	+0.004259	+0.002906	+0.004907	—0.188133	—0.135814
$(y_1 + y_2)$....	+0.845289	+0.231468	—0.255306	—1.282539	+0.232643	—0.439287	—0.046389

TABLE 20. TESTS OF SIGNIFICANCE OF REGRESSION OF THE WHITE OAK DATA ON ASHEVILLE, N. C., RAINFALL COEFFICIENTS

Group combination and source of variation	Degrees of freedom	Sum of squares	Mean square
Difference between groups i.e., $(y_1 - y_2)$:			
Regression on α_0 only.....	1	17.2	17.2[1]
Increase with $\alpha_1 \ldots \alpha_6$.....	6	908.7	151.5[1]
Regression on $\alpha_0 \ldots \alpha_6$.....	7	925.9	132.3[1]
Deviation from regression.....	22	14,395.1	654.3
Total.....	29	15,321.0	
Sum of both groups i.e., $(y_1 + y_2)$:			
Regression on α_0 only.....	1	32,675.2	32,675[2]
Increase with $\alpha_1 \ldots \alpha_6$.....	6	75,551.6	12,592[3]
Regression on $\alpha_0 \ldots \alpha_6$.....	7	108,226.8	15,461[2]
Deviation from regression.....	22	112,159.2	5,098
Total.....	29	220,386.0	

[1]Not significant.
[2]Significant at the 5 percent level.
[3]Significant at slightly higher than the 5 percent level.

freedom were used in fitting trend curves of degree 2 to the original data, after 1 is absorbed by the general mean. Seven degrees of freedom are used in fitting the regression on $\alpha_0 \ldots \alpha_6$. Deviations from regression are therefore based upon the remaining 22 degrees of freedom.

For the data $(y_1 - y_2)$ the mean square due to regression on α_0 alone, to the remaining effect of $\alpha_1 \ldots \alpha_6$, and to the regression on $\alpha_0 \ldots \alpha_6$ are all, in fact, less than the mean square of deviations from regression. The data therefore contain conclusive evidence that the two groups of oak are

not reacting to the precipitation distributions in perceptibly different ways.

The best estimate of the effect of precipitation distribution on either group of the oak data is, in consequence, contained in the regression of $(y_1 + y_2)$ on the precipitation coefficients. Tests pertaining thereto are contained in the lower half of Table 20. The regression on $\alpha_0 \ldots \alpha_6$ is significant. The regression on α_0 alone is also significant.

The evidence is therefore convincing that width of annual ring of the oak depends upon both the aggregate amount of precipitation to which it is exposed during the 15-month period preceding the end of its growing season, and upon how the precipitation is distributed within the period. There is no evidence, however, that the two groups of trees into which the data were subdivided, have been affected differently by either the aggregate precipitation or its distribution.

The extent of precipitation influence may be illustrated by graphic representation of the effect of an additional inch of precipitation per month, according to the months of the period, upon the width of annual ring. Putting the coefficients $a_0, a_1, \ldots, a_6$, for the data $(y_1 + y_2)$ as derived from Table 19, into equation (2) and dividing by 2 we have

$$\frac{1}{2}(Y_1 + Y_2) = \frac{1}{30}\left\{0.845289 + 0.231468\left[X_1(t)\right] + \ldots . - 0.046389\left[X_6(t)\right]\right\}$$

the functions $X_1(t) \ldots X_6(t)$ being taken from Lorenz's tables (1931). The calculated values are then plotted on t. Since precipitation is in terms of hundredths of inches per month, and the logarithms of relative annual ring width residuals used in the calculations have been multiplied by 10^3, the calculated values are divided by 10 to show the average effect of an additional inch of precipitation per month on unit logarithm of annual ring width. But rather than show resulting logarithms on arithmetic scale, the percentage deviation from the average ring width—derived from the antilogarithms—are presented in Figure 13. In this figure the curve of each group is shown for comparison with the average of both groups. The average curve, of course, portrays the best estimate of precipitation effect, because the other two do not differ significantly.

The middle curve of Figure 13 thus represents the average benefit to the annual ring width of 1 inch of precipitation per month, during the 15-month period, in excess of each monthly average as given by the precipitation distribution curve of Figure 12, for Asheville, North Carolina. Change in sign of the ordinate scales would, of course, represent corresponding average damage chargeable to 1 inch of precipitation per month below its monthly average. In like manner, the best estimate of annual ring width as a result of no change from the monthly averages—that is, the average precipitation distribution itself—would be zero deviation from the general averages given at the bottom of Table 3.

Figure 13 shows that the most beneficial distribution of precipitation for white oak as represented by these data, is a rather dry August and September followed by a wet winter, spring, and early summer.

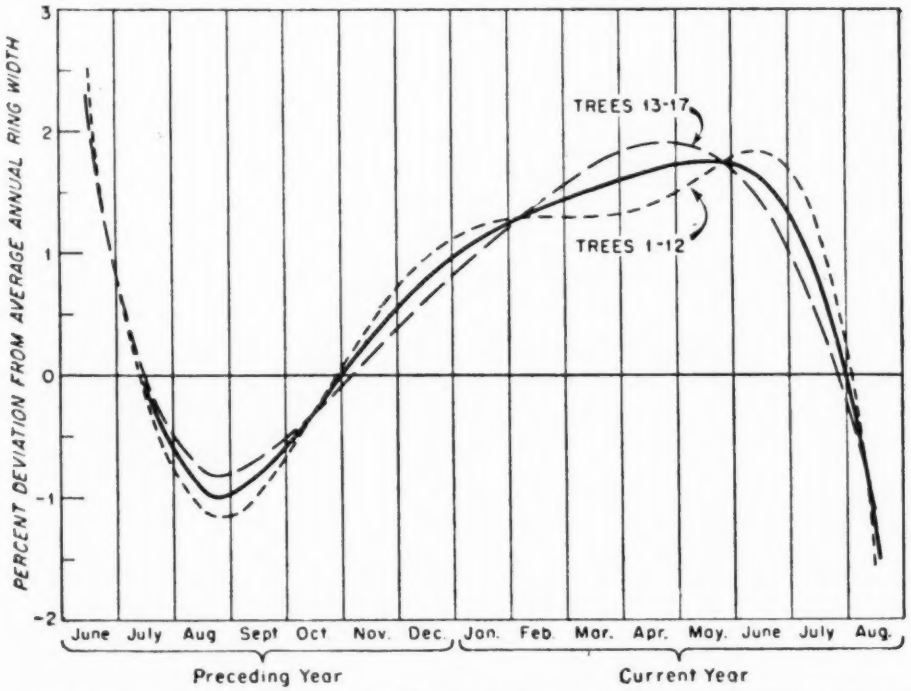

FIG. 13. Average effect of 1 additional inch of precipitation per month on the width of annual ring of white oak near Asheville, N. C.

LONGLEAF PINE IN FLORIDA

The longleaf pine data were submitted to analyses similar to those employed on the oak. Regression equations were calculated from the data of each group—Lake City, Gainesville, Jacksonville—separately, as each was subjected to precipitation distributions peculiar to its own locality. A common regression equation was then calculated from the data of the combined groups.

Division of total sum of squares into pertinent portions resulting from each analysis is given in Table 21. It might be pointed out, again, that the degrees of freedom upon which the total sum of squares of the analysis of each group is based is the number of annual observations less $(d + 1)$ degrees of freedom, where d is the degree of trend used in removing the effect of slow change in annual ring width. The number of observations available are 28, 38, and 42 for Lake City, Gainesville, and Jacksonville, respectively. The degrees of freedom absorbed by the trend curves are, in turn, 4, 6, and 3. Hence the sum of squares for the total of each group in the present analyses are 23, 31, and 38. These are listed in Table 21.

Each group may, of course, be tested individually. There is some advantage, however, in searching for consistency of precipitation effect on the annual ring width of the three groups. Accordingly, pertinent quantities, drawn from Table 21, are assembled in Table 22. The first two sums of squares in the latter table, containing the analysis of the α_0 effects, are taken from the first line of each part of Table 21.

TABLE 21. DIVISION OF THE SUMS OF SQUARES OF THE LONGLEAF PINE DATA FROM FLORIDA INTO PARTS DUE TO, AND INDEPENDENT OF, THE RAINFALL COEFFICIENTS AT NEAREST STATIONS

Tree group and source of variation	Degrees of freedom	Sum of squares
Lake City group:		
Regression on α_0 only	1	19,565.1
Increase with $\alpha_1 \ldots \alpha_6$	6	9,678.9
Regression on $\alpha_0 \ldots \alpha_6$	7	29,244.0
Deviation from regression	16	33,819.0
Total	23	63,063.0
Gainesville group:		
Regression on α_0 only	1	2,291.3
Increase witl. $\alpha_1 \ldots \alpha_6$	6	5,014.5
Regression on $\alpha_0 \ldots \alpha_6$	7	7,305.8
Deviation from regression	24	61,153.2
Total	31	68,459.0
Jacksonville group:		
Regression on α_0 only	1	19,376.0
Increase with $\alpha_1 \ldots \alpha_6$	6	21,148.0
Regression on $\alpha_0 \ldots \alpha_6$	7	40,524.0
Deviation from regression	31	134,841.1
Total	38	175,365.1
All groups combined:		
Regression on α_0 only	1	18,352.7
Increase with $\alpha_1 \ldots \alpha_6$	6	12,624.4
Regression on $\alpha_0 \ldots \alpha_6$	7	30,977.1
Deviation from regression	85	275,909.9
Total	92	306,887.0

For the Lake City group	19,565.1	with 1 degree of freedom
For the Gainesville group	2,291.3	with 1 degree of freedom
For the Jacksonville group	19,376.0	with 1 degree of freedom
For the three groups individually	41,232.4	with 3 degrees of freedom
For the three groups combined	18,352.7	with 1 degree of freedom
Differential effect on groups	22,879.7	with 2 degrees of freedom

Similarly the sum of squares due to $\alpha_1 \ldots . \alpha_6$ on the combined group—that is, 12,624.4 which is entered directly from Table 21 to Table 22—is less than the corresponding pooled sum of squares of the individual groups by 23,217.0. The latter quantity is therefore due to the differental effect of the precipitation coefficients $\alpha_1 \ldots . \alpha_6$ on the groups, and this is also entered.

The fifth line of Table 22 contains the pooled sum of squares of deviation from individual group regressions. It is the part of the pooled total sum of squares (recorded in the bottom line of the table) which is independent of precipitation, as based upon the pooled 71 degrees of freedom.

As the tabulation brings out, the average α_0 effect within groups is significant; but so, also, is the differential effect of α_0 on the groups. The effect of the distribution coefficients $\alpha_1 \ldots \alpha_6$, however, are not significant. It is to be concluded, therefore, that the width of annual ring is a function of average precipitation per month—or aggregate over the 15-month period—but not of its distribution within the period; and that there is a significant differential effect of precipitation, in amount but not in distribution, on the several groups.

TABLE 22. FINAL ANALYSIS OF VARIANCE, AND TESTS OF SIGNIFICANCE OF THE REGRESSIONS OF LONGLEAF PINE ON THE PRECIPITATION COEFFICIENTS AT NEAREST STATIONS IN FLORIDA

Source of variation	Degrees of freedom	Sum of squares	Mean square
α_0 Average effect within groups	1	18,352.7	18,353[1]
Differential effect on groups	2	22,879.7	11,440[1]
$\alpha_1 \ldots \alpha_6$ Average effect within groups	6	12,624.4	2,104[2]
Differential effect on groups	12	23,217.0	1,935[2]
Deviation from individual group regressions	71	229,813.2	3,237
Total within groups	92	306,887.0	

[1]Significant at the 5 percent level.
[2]Not significant.

The regression functions in the form of equation (2) are pictured in Figure 14. The departure of each curve from the horizontal line representing its own average level cannot be shown to be due to variation in the effect of monthly precipitation. Furthermore, the negative average level of the Gainesville regression is not a significant departure from zero, as the test of its own α_0 effect, by means of the data in the Gainesville group of Table 21, would demonstrate. Its departure from the average level of the Lake City and Jacksonville regressions, however, is probably real, in the light of the significant differential effect of α_0 on the groups.

The best estimate of precipitation upon the Lake City and Jacksonville longleaf pine is derived from the regression on α_0 only, that is

$$\frac{S\left[\alpha_0(y - M_y)\right]}{S(\alpha_0 - M_{\alpha_0})^2}$$

in which numerator and denominator represent the pooled sums of products and sums of squares, respectively, for the two groups. Upon calculation, this value is found to be 0.50 percent increase in annual ring width per inch increase of precipitation per month.

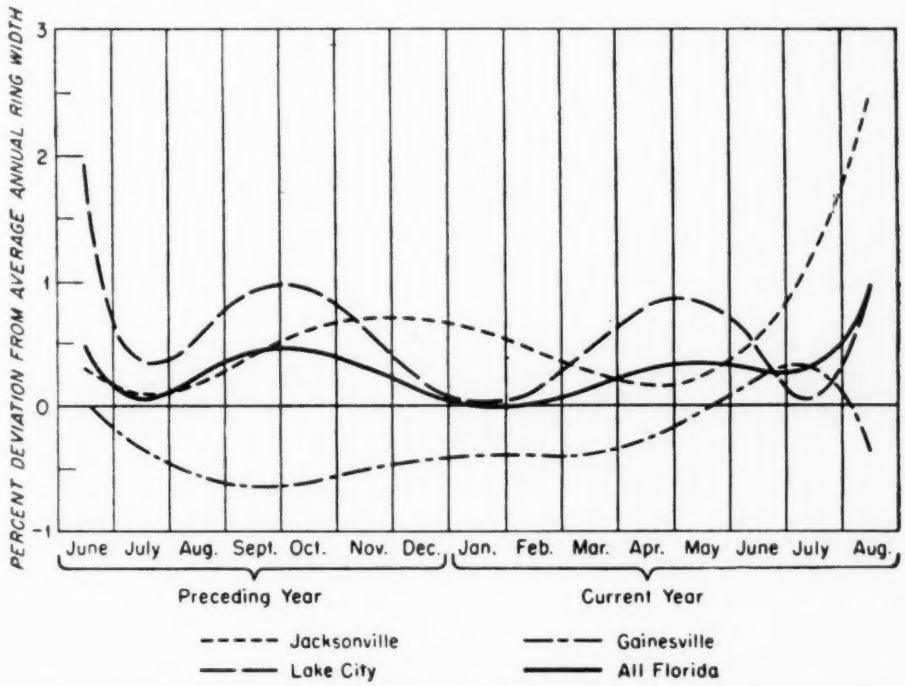

FIG. 14. Average effect of 1 additional inch of precipitation per month on the width of annual ring of Florida longleaf pine.

SHORTLEAF PINE IN VIRGINIA

The "dead" and "live" tree groups of shortleaf pine in Virginia were subjected separately to regression on the precipitation coefficients at nearby Washington, D. C. A common regression based upon the combined data of the two groups is not used; for annual ring data from the years 1874 to 1932 are represented in both groups, while the other years between 1854 and 1935 are represented in one or the other group only. Hence an analysis of differential effect of precipitation distribution upon the two groups is not to be obtained by a simple classification of the sums of squares involved. As it turns out, however, the interpretation of results obtained is very simple.

The division of the sums of squares into portions due to, and independent of, the precipitation coefficients is presented in Table 23 for each group. Cursory examination of the mean squares of the "dead" tree group affords suffi-

cient evidence of complete absence of significant precipitation effects. The mean squares due to regression are less than the mean square of the deviations.

It was pointed out previously that this group of shortleaf pine had been growing upon a lower slope. It may be, therefore, that the soil moisture available to its root systems was maintained at sufficient levels independently of precipitation fluctuations.

In the "live" tree group, on the other hand, the regression on α_0—average precipitation per month during the 15-month period—is probably real, for it is significant at the 5 percent level. The effect of precipitation distribution upon this group, however, is negligible.

Figure 15 shows graphically the observed effect of an additional inch of precipitation per month on the relative growth of annual ring width for the shortleaf pine data.

TABLE 23. DIVISIONS OF SUMS OF SQUARES OF THE SHORTLEAF PINE DATA INTO PARTS DUE TO, AND INDEPENDENT OF, THE RAINFALL COEFFICIENTS AT WASHINGTON, D. C.

Tree group and source of variation	Degrees of freedom	Sum of squares	Mean square
"Dead" tree group:			
Regression on α_0 only	1	15.9	16[1]
Increase with $\alpha_1 \ldots \alpha_6$	6	22,789.8	3,798[1]
Regression on $\alpha_0 \ldots \alpha_6$	7	22,805.7	.....
Deviation from regression	68	400,884.2	5,895
Total	75	423,689.9	
"Live" tree group:			
Regression on α_0 only	1	21,229.5	21,230[2]
Increase with $\alpha_1 \ldots \alpha_6$	6	26,418.4	4,403[1]
Regression on $\alpha_0 \ldots \alpha_6$	7	47,647.9	.....
Deviation from regression	51	250,517.5	4,912
Total	58	298,165.4	

[1]Not significant.
[2]Significant at the 5 percent level.

HEMLOCK IN NEW HAMPSHIRE

Unlike the data for the other species, hemlock comprises a single group. As there is no advantage in transforming its residuals from the average trend curve of the group to the logarithmic scale they are maintained in the original scale of hundredth millimeters.

The division of the hemlock sum of squares into portions due to, and independent of, the precipitation coefficients at Hanover, New Hampshire, are shown in Table 24. The total sum of squares is based upon 76 degrees of freedom among the 87 annual ring residuals, since 11 degrees of freedom were absorbed in fitting the trend curve of degree 10. It is at once evident

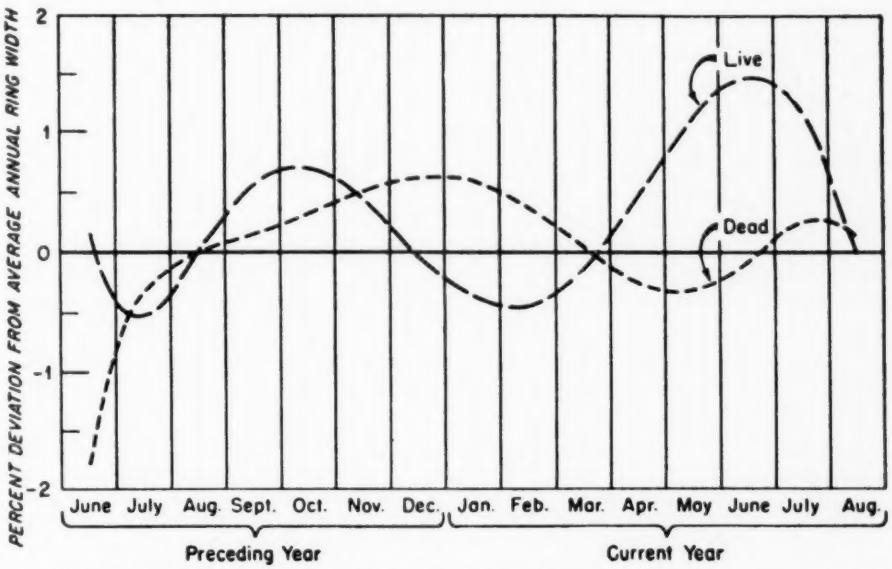

FIG. 15. Average effect of 1 additional inch of precipitation per month on the width of annual ring of shortleaf pine near Washington, D. C.

that there is a complete lack of significant precipitation effect, as mean squares due to regression are less than the mean square of the deviations.

The graphical representation of the effect of an additional inch of precipitation per month is presented in Figure 16.[6] It is to be observed that additional precipitation during the months of July and August of both preced-

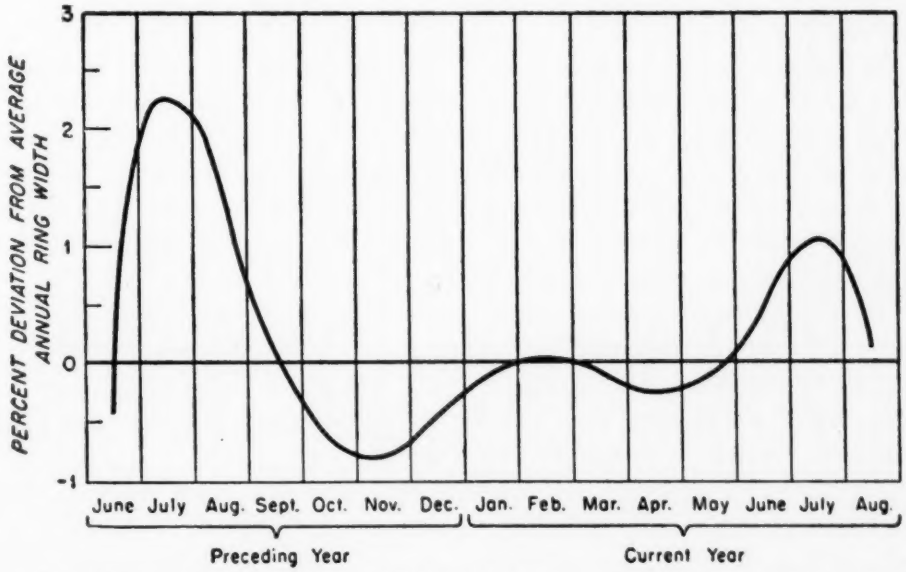

FIG. 16. Average effect of 1 additional inch of precipitation per month on the width of annual ring of hemlock near Hanover, N. H.

[6] The ordinate of Figure 16 has been transcribed to the percentage scale in harmony with corresponding figures of other species.

ing and current years tends to increase the width of the current annual ring. It may be that the failure of these observed effects to turn up significant is ascribable to the known unusual tolerance of the species to competition of its associates. Variability in competition to which individual hemlock trees are subjected in different years may have overshadowed the benefit of precipitation rather thoroughly.

TABLE 24. DIVISION OF SUMS OF SQUARES OF THE HEMLOCK DATA INTO PARTS DUE TO, AND INDEPENDENT OF, THE RAINFALL COEFFICIENTS AT HANOVER, NEW HAMPSHIRE

Sources of variation	Degrees of freedom	Sum of squares	Mean square
Regression on α_0 only	1	47,914.90	47.915
Increase with $\alpha_1 \ldots \alpha_6$	6	110,736.08	18,456
Regression of $\alpha_0 \ldots \alpha_6$	7	158,650.98	22,664
Deviation from regression	69	6,463,110.70	93,668
Total	76	6,621,761.68	

SUMMARY

Annual ring width variation, even in the dominant stand of a pure forest type, is marked by notable heterogeneity. In order to investigate the effects of meteorological elements upon annual ring width it is imperative that the total variation among ring widths of a number of sample trees be arranged according to the sequence of years for which data are at hand, so as to segregate therefrom statistically homogeneous material for the study of meteorological effects.

This process is part of an analysis through which the total variation is divided into portions whose causes, or groups of causes, are assignable. One source of heterogeneity is the complex of inherent and longtime environmental factors which control the average ring widths of individual trees over the entire span of years represented by the data; another is the influence of age progression and site quality trend which brings about slow changes in growth common to the dominant stand.

Annual variation is made up of statistically homogeneous material common to the trees of the dominant stand, and is due mostly to fluctuations of climate. A remaining unaccounted-for part peculiar to each ring, is the natural outcome of variation in the width of individual rings at different points along their perimeters, and to errors of measurement.

The data are made up of 2 groups of white oak from western North Carolina, 3 groups of longleaf pine from Florida, 2 groups of shortleaf pine from northern Virginia, and a group of hemlock from New Hampshire. Out of the total sum of squares among the annual ring widths of the separate groups, only from 3 to 12 percent is in common annual variation ascribable to fluctuations of climate. The need for isolating these relatively small por-

tions from the totals in order to evaluate the effect of a single meteorological element, precipitation, is obvious.

The method used is that of regression analysis. The dependent variate of each group is average residual of the tree rings from trend for each year of the sequence. The independent variates were derived from the monthly precipitation records at nearest United States Weather Bureau stations. Specifically, they are coefficients of orthogonal polynomials of degree 6, which express precipitation distribution during the 15-month periods from June of a preceding year to August, inclusive, of a current year, for each current year of annual ring growth represented by the data.

The analyses permitted the division of that section of annual ring width variation which is due wholly to precipitation into 2 parts; namely, a part due to average monthly precipitation regardless of how it is distributed over the 15-month period, and a remaining part due only to its distribution.

The longleaf pine from Gainesville, Florida, one group of shortleaf pine from Virginia, and the hemlock from New Hampshire were not affected to any significant extent by either the average monthly precipitation or its distribution over the 15-month period. The longleaf pine from Lake City and from Jacksonville, Florida, and the second group of shortleaf pine from Virginia were found to be dependent on amount of precipitation, but not to any significant extent upon its distribution, for added width of annual ring. The oak data from North Carolina were sensitive to both.

By means of tables of orthogonal functions the regression equation of each group is made to express the average effect of an added inch of precipitation per month during the 15-month period on width of annual ring. These are presented graphically.

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A QUANTITATIVE STUDY OF TRUE-PRAIRIE VEGETATION AFTER THREE YEARS OF EXTREME DROUGHT

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A QUANTITATIVE STUDY OF TRUE-PRAIRIE VEGETATION AFTER THREE YEARS OF EXTREME DROUGHT[1]

INTRODUCTION

Current opinion and activity toward revegetating exploited and submarginal grasslands justify the expenditure of considerable time in improving our knowledge of the behavior of native species under the stress of drought. The drought of 1936 equaled or surpassed in severity the great drought of 1934. This study is intended as another link in the chain of investigations concerning the composition, structure, and behavior of the rapidly disappearing remnants of true prairie. Attention is focused upon the relative capacity for survival and reproduction shown during drought by prairie species. That even a single species may well merit close and continued study is shown in such investigations as those of Savage (1934), Savage and Jacobson (1935), and Humphrey (1937).

A number of papers emanating from various parts of the grassland area have set forth the results of the drought of 1934. Pechanec *et al.* (1937) found that perennial herbs were reduced 25 percent on the upper Snake River plains of Idaho. The injury was not permanent as shown by the fact that in 1935 the number was higher than before the drought. However, the principal forage grasses recovered only slightly. In southeastern Montana, forage grasses were injured far beyond their ability to recover during the favorable season of 1935. Blue grama *(Bouteloua gracilis)*, western wheat grass *(Agropyron smithii)*, and buffalo grass *(Buchloe dactyloides)* were reduced to 25 percent, but Sandberg bluegrass *(Poa secunda)* nearly trebled its holdings (Ellison and Woolfolk 1937). In the same state, overgrazed prairie pastures showed recovery during drought under correct utilization (Bell 1935). Beath (1935) reported the ranges of eastern Wyoming to be in good condition in June, 1935. However, Allred (1935) states that in eastern Colorado blue grama and buffalo grass had been greatly injured and that 40 percent of the forage grasses had been killed.

The present study is most closely related to the work of Weaver and Albertson (1936) and Weaver, Stoddart, and Noll (1935). They found that among native grasses the worst killing was correlated with shortest root systems. Western wheat grass and aster *(Aster multiflorus)* had increased. That soil moisture was the critical factor was shown by the normal activity of watered plants during the period of greatest stress. The investigations of Weaver (1919, 1920) and of Nedrow (1937) on the root development and depth of efficient absorption by prairie plants have made possible the inter-

[1] Contribution from the Department of Botany, University of Nebraska, No. 109. The writer was aided in this research by a grant from the Nebraska Academy of Sciences.

pretation of drought behavior of most native plants in terms of available soil moisture. The effects of any disturbance can be well known only in so far as the original or normal condition is understood. The bases of comparison for this study have been provided by the extensive survey of Weaver and Fitzpatrick (1934) and the intensive work of Steiger (1930).

It is a pleasure to acknowledge the assistance given the writer by Dr. J. E. Weaver. It was he who suggested the problem and whose thorough familiarity with the vegetation made possible the identification of species in all stages of development.

PROCEDURE

In order to obtain an average of conditions and to study behavior of various species under different local conditions of soil and climate, selection was made of nine prairies. Eight of these had been previously described. The most distant is 110 miles southwest of Lincoln and the two nearest each other are 10 miles apart but on quite different soil types (Fig. 1).

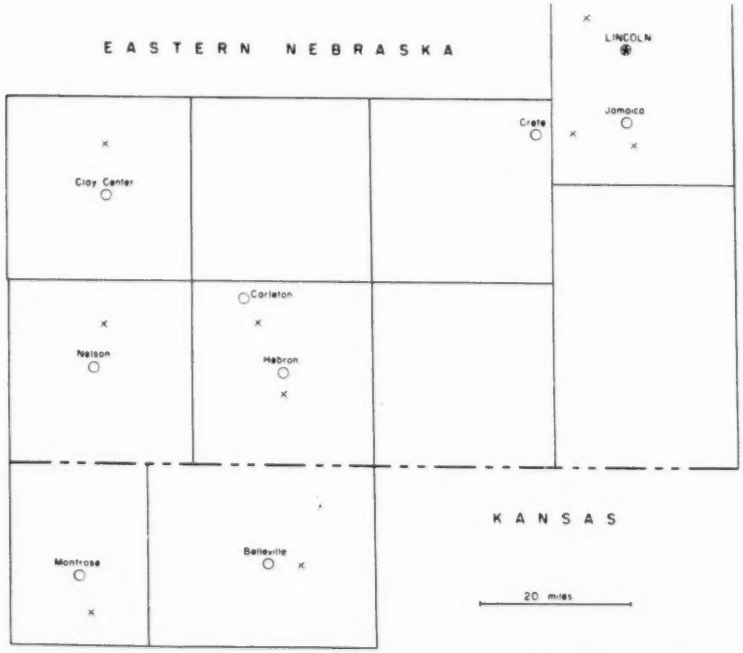

FIG. 1. Map showing location of prairies studied (x) and the towns near which they lie (o).

Field work was carried on during the summers of 1936 and 1937. Studies were made at three periods each season, always with the assistance of one or two competent helpers. After careful reconnaissance, enough permanent plots were established to sample each of the principal types of vegetation. The plots were usually placed on the tension line between alternes and thus included two types. The size and shape of the plots varied with the kind and

density of the vegetation, but the meter quadrat proved most satisfactory. The list or census method was employed, owing to the dominance of the sod form and to the belief that this is the most accurate method and the only one which can be used by subsequent workers with equal accuracy. In a few instances where stolons were present or short grasses were especially dense, estimated percent of cover instead of number of stems was recorded. In such cases the number of stems required to form one percent basal cover was determined. Where short-lived annuals were unusually dense, they were ordinarily not counted; instead the number of square decimeter units occupied by them was recorded. The plots were marked at diagonally opposite corners by a square oak stake and a round iron one, each 15 inches long, and driven even with the soil surface in order not to interfere with mowing. A conspicuous piece of red rubber was embedded with an end exposed just outside the wooden stake and the position of the latter established by angle and distance from a land mark and when practicable from one other plot.

Under the stimulus of such work as that of Cain (1931), Emmett and Ashby (1934) and others, an effort was made to correlate vegetation type with chemical and physical factors of the soil. Soil samples were taken from different types of vegetation on prairies where alternes were the sharpest, and tests were made for the amount of chlorides by the method described by Weaver and Clements (1938).

Determinations of available moisture were made from samples from depths of 3 to 4 feet twice each season, and on three prairies to depths of 8 to 15 feet once each August. Only water in excess of the hygroscopic coefficient was considered available. Tests for the presence of carbonates and for the degree of acidity by using the colorimetric method were also made on numerous samples from different alternes.

The species were recorded on five prairies each year in 25 to 100 semicircular temporary plots .8 sq. m. in area and spaced at fixed intervals along predetermined lines. The interval and number of plots were governed by the size of the tract and general uniformity of the vegetation. This was done in order to determine whether drought causes changes in distribution of dominants concomitant with changes in abundance.

Notes were taken concerning the condition of the important species, and an estimate of the abundance of each species observed was recorded on a 5-point scale. A prepared form containing the names of 120 species most important on upland prairies (Weaver and Fitzpatrick 1934) was used. The figure 1 placed after the name of a species indicated that it was very abundant; 2 indicated abundant; 3, common; 4, infrequent; and 5, rare.

Meteorological data were obtained from United States Weather Bureau records for the station nearest the prairie under discussion, and behavior of the vegetation was interpreted in the light of these data and conditions of soil.

Under normal precipitation, very pervious soils would be expected to

contain more moisture than less pervious ones. Experiments were performed to ascertain differences, if any, in the degree to which different types of prairie vegetation influence the absorption of water. This was done on seven prairies in a total of twelve types of vegetation. Well developed bunches of grass, stems of forbs, sodded areas or bare areas only a few feet distant were selected. Cylinders were made from 15-inch sections of seamless steel tubing 4 inches in diameter and sharpened at one end. These were forced into the soil vertically to depth of 14 inches. A coating of light motor oil inside and

FIG. 2. Equipment for measuring the rate of infiltration of water into the soil pictured in use on the Belleville, Kansas, prairie. One cylinder is ready to receive the first of 4 inches of water, and another is in position to be forced into the soil.

out, combined with the sharpness of the cutting edge and the thinness (.1 inch) of the wall of the cylinder reduced to a minimum the possibility of altering the structure of the enclosed soil. Two heavy steel augers anchored in the soil were employed to support a heavy, steel-faced oak beam under which the jack was set as described by Weaver, Hougen, and Weldon (1935) (Fig. 2). The cylinders were usually paired at each setting of the augers. Each surface inch of water was added separately and a record kept of the time of watering and of the disappearance of the water into the soil. All tests were made in replications of four cylinders. On completion, the cylinders were removed without disturbing the sod by means of an especially designed jack. It consisted of a metal disk at the end of a strong screw which pressed downward on the soil within the cylinder while a cross-bar fitting into the holes in the cylinder wall pulled the latter out of the ground.

Musgrave (1935) used similar equipment to study the relation of infiltration to runoff and erosion. He states that the method gave results "in substantial agreement" with those obtained by the use of lysimeters which measure percolation and runoff. Auten (1933) also used cylinders to learn that overgrazing and surface fires reduce absorption. Smith *et al.* (1937) found that manuring increased the rate of infiltration in cultivated fields. Great differences between cylinders were explained by the presence of wormholes and decayed stalks of corn.

Finally, in order to learn what potential invaders were present in drought-bared areas, 20 to 25 random samples of bare soil to a depth of two inches were taken with a trowel on each of five prairies. The samples from each prairie were thoroughly mixed and placed in five flats in the greenhouse. A record was made of the number and species of all seedlings appearing during a period of five months.

RESULTS

JAMAICA PRAIRIE

This prairie has been described (Weaver and Albertson) as "65 acres of rather low, level land lying north of a stream bordered by postclimax woodland 12 miles south of Lincoln." The 20- to 30-foot trees along the stream, Salt Creek, shelter the lower part of the prairie from the desiccating south winds (Fig. 3). The soil of the lowland is Wabash silt loam. That

FIG. 3. Jamaica prairie in 1937 showing a broad alterne of wheat grass (dark) occupying most of the low ground of the prairie. The wheat grass was interrupted by smaller alternes of big bluestem (Fig. 7).

of the south-facing slope on the north, which forms about 10 percent of the area and ascends 20 feet above the general level, is Waukesha silt loam.

Prior to 1934 big bluestem *(Andropogon furcatus)*[1] furnished "60 to 90 percent" and little bluestem *(A. scoparius)* on the upland "as much as 25 percent of the cover." Considerable prairie dropseed *(Sporobolus heterolepis)* was present in alternes, and Kentucky bluegrass *(Poa pratensis)* was of general distribution. Wheat grass, blue grama, and buffalo grass were restricted

[1] The nomenclature here is that employed by Weaver and Fitzpatrick (1934).

to a few small alternes. Among the forbs, aster, Missouri goldenrod *(Solidago glaberrima)*, and prairie rose *(Rosa arkansana)* were most abundant, with prairie sage *(Artemisia gnaphalodes)* and rough pennyroyal *(Hedeoma hispida)* being less abundant.[2]

The present study of this prairie was begun in June, 1936. Big bluestem was found to be greatly injured, being represented more by dead crowns and exposed rhizomes than by living shoots. It no longer ranked first in abundance, but was replaced in this respect by wheat grass. The latter formed a broad belt diagonally across the prairie (shown by the darker area in the middle of Fig. 3). It had its best development on poorly drained areas and formed an open stand over most of the former area of little bluestem. It also had many other foci of dissemination established over the low ground, even to within 40 yards of the wooded creek bank, but was fruiting only on the ground invaded during previous years.

Little bluestem was almost entirely absent where it formerly made up 25 percent of the cover. Prairie dropseed was widely distributed and commonly represented by large half- or more than half-dead bunches. June grass *(Koeleria cristata)* and needle grass *(Stipa spartea)* were both abundant and conspicuous.

The small interstitial panic grasses *(Panicum scribnerianum* and *P. wilcoxianum)*, though not abundant, were so uniformly distributed that nearly every square meter contained at least a few plants. The same was true of Kentucky bluegrass and seedlings of goat's-beard *(Tragopogon pratense)*. Canada bluegrass *(Poa compressa)* was scattered over most of the prairie, except the upper slope, but seemed most closely associated with *Agropyron smithii*. Six-weeks fescue *(Festuca octoflora)* was not seen and side-oats grama *(Bouteloua curtipendula)* was rare.

Aster multiflorus was the most abundant perennial forb. Individuals of all heights up to 20 inches formed open to dense stands, both pure and mixed, everywhere except in the best *Andropogon furcatus* along the creek and in alternes of pure *Agropyron smithii, Buchloe dactyloides,* and *Bouteloua gracilis*. It was not difficult to find square meter areas containing 250 to 300 stems. Daisy fleabane *(Erigeron ramosus)* ranked next to aster in abundance and was even more conspicuous on higher ground where the severest drought injury had occurred.

Solidago glaberrima was common and widely distributed although largely defoliated by grasshoppers. The same was true of upland prairie sunflower *(Helianthus rigidus)* and Tragopogon seedlings, the former being less abundant. Withered seedlings of wild lettuce *(Lactuca scariola)* were very abundant but larger plants were uncommon.

As on most prairies, the major grasses as well as some of the forbs were largely aggregated into distinct minor communities of relatively pure popula-

[2] Information as to condition of prairies before 1934 is drawn from Weaver and Albertson (1936) and from Dr. Weaver's original prairie notes.

tion. This marked alternation is attributable either to local soil differences or to chance priority followed by effective aggregation and successful competition with neighbors and would-be invaders.

Chemical and moisture analyses of soil samples from within wheat-grass alternes and adjacent areas of big bluestem showed only a few minor differences. Assuming the chlorides present to be in the form of NaCl, the highest salt content (540 parts per million) was in the densest, poorest drained wheat-grass alterne, and an average of all series down to 2 feet showed Agropyron soil twice as salty (210 p.p.m) as that underlying *Andropogon furcatus* (110 p.p.m). However, a younger Agropyron alterne yielded at the 0-6-inch depth the smallest amount of salt (30 p.p.m.). The soil varied in acidity from pH 4.7 at the surface to pH 6.6 at a depth of 2 feet. An average of all samples from wheat-grass soil equaled pH 5.1 as compared with pH 4.9 in the big bluestem type, a difference which may easily have resulted from errors in determination.

No positive test for carbonates was obtained. Available soil moisture ranged from a negative amount in the surface six inches to about 12 percent at the three-foot level. In two series for which hygroscopic coefficients were determined, more available moisture was present under big bluestem than under wheat grass at each depth except in the surface six inches where none was available in 1936. This difference increased downward at least to 3 feet. In late August of the following year, however, more moisture was present in the Agropyron area because the grass had lain dormant since being mowed two months earlier (Table 1). At a depth of two feet under wheat-grass sod, the soil was lighter in color, harder when dry, less pervious when pinched under water, and stickier when wet than under that of big bluestem.

In the vicinity of Lincoln in 1936, the rainfall deficiency was nearly one-third greater than in 1934 (Fig. 4). Extremes of temperature and humidity also deviated widely from normal in 1936. February and July were the coldest and hottest, respectively, ever recorded in Nebraska. July was also the driest, and August the hottest on record. As shown in Figs. 4 and 5, July (7) was 10 degrees warmer than normal with the average percentage relative humidity 22 lower and rainfall more than 3.5 inches below normal.

TABLE 1. PERCENTAGE OF AVAILABLE SOIL MOISTURE IN ALTERNES OF BIG BLUESTEM AND WESTERN WHEAT GRASS SIX FEET APART

Depth in feet	ANDROPOGON				AGROPYRON			
	Hygroscopic coefficient	1936	1937		Hygroscopic coefficient	1936	1937	
		June 25	June 19	Aug. 23		June 25	June 19	Aug. 23
0-.5.....	13.7	—3.4	14.8	2.7	12.0	—2.5	13.0	4.5
.5-1.....	10.7	1.2	15.8	4.0	10.2	0.2	7.7	7.9
1-2.....	13.0	5.6	5.9	3.0	14.5	2.5	4.2	3.1
2-3.....	12.7	7.7	11.0	3.4	11.3	7.1	3.8	4.6

Rainfall for the three summer months was 73 percent of normal in 1937 but only 24 percent in 1936. The maximum temperature in 1936, 115° F., was 3 degrees higher than in 1934. Evaporation at Lincoln from an open pan from April to October was 78.1 inches in 1934, or 9 inches more than in 1936. The mean vapor pressure deficit was higher than normal in 1936 but, except for July, lower than that of 1934 (Fig. 5). That summer humidity was far below normal in 1936 may be seen by comparing the positions of numbers 6 to 8 in Figure 5.

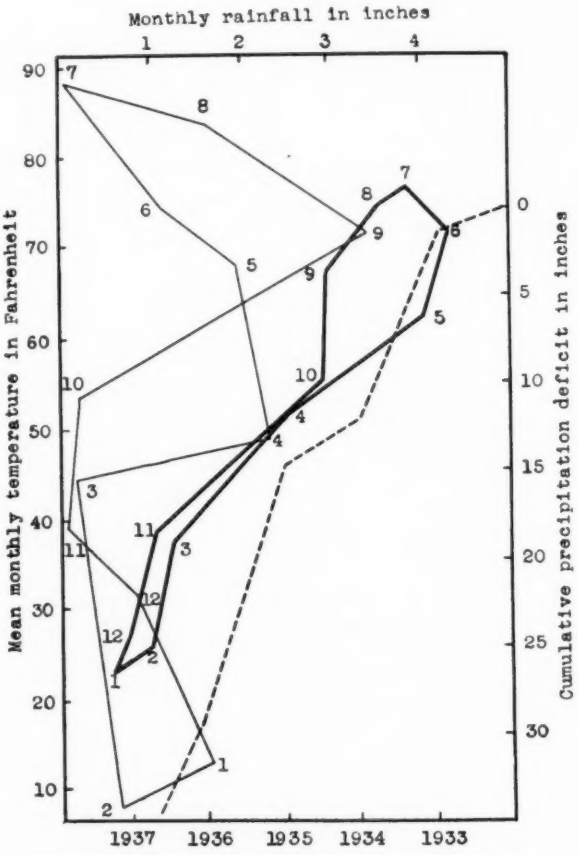

FIG. 4. Hythergraph showing mean monthly temperature and rainfall for 1936 (light line) and for the 50-year period (heavy line). Numbers 1 to 12 represent months. Broken line shows cumulative precipitation deficit (in inches on right) from January 1, 1933, to August 31, 1937.

Careful counts of rooted shoots of all species in 13 plots were made during the last week in June, 1936 and 1937, and the principal data are shown in Table 2.

The generally vigorous condition of the vegetation in June, 1937, as well as the nearly normal moisture conditions of soil and air (Figs. 4 and 5, and Table 1) lead to the conclusion that losses in number of stems were due to death of their underground parts, rather than to mere inhibition of growth. In May, many species of the vernal aspect appeared highly vigorous. Several carices were in flower, wheat grass had definitely extended its territory, aster was more abundant, and the yellow flowers of goat's-beard were beginning to appear on nearly every square meter (Fig. 6). Most of the bunches of prairie dropseed were dead, especially in the dense new alterne of *Agropyron smithii*. Rhizomes of the latter had penetrated many of the bunches and pierced the dead crowns with their sharp new spears. It was possible to proceed in one general direction for 79 paces through this area stepping only upon these totally dead crowns.

The part of this prairie containing most of the plots was mowed early (June 13) in order to improve the palatability of the wheat-grass hay. This

naturally increased the difficulty of identification in quadrating and made necessary the exclusion of data on a few of the rarer species. Accuracy in listing of others was not prevented.

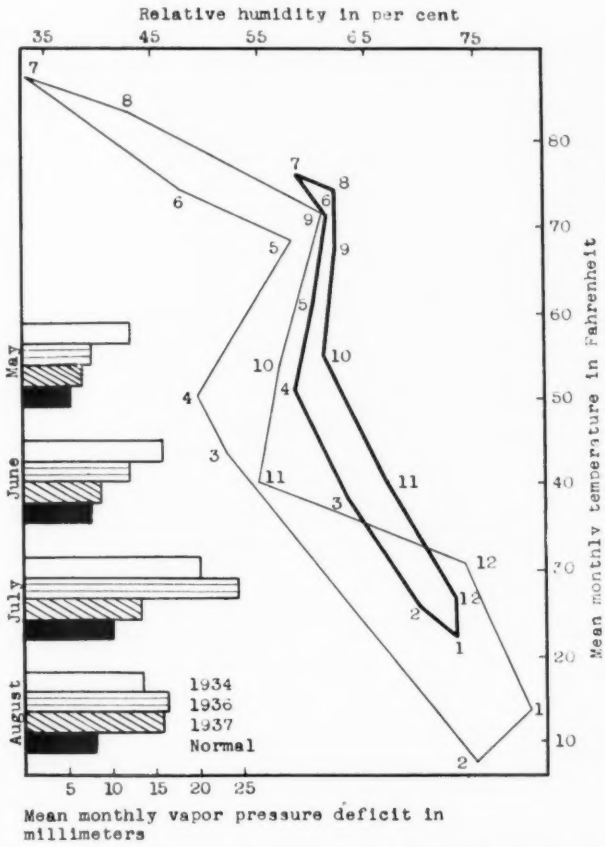

FIG. 5. Climograph of mean monthly relative humidity and temperature for 1936 (light line) and for a 50-year period (heavy line) at the Jamaica prairie. Numbers 1 to 12 represent months. Bar graph shows mean monthly vapor pressure deficits for 4 summer months in 1934, 1936, 1937, and the 50-year period. Humidity and vapor pressure calculations are based on averages of 7:00 A.M., 12:00 Noon, and 7:00 P.M. readings.

Two weeks after mowing, the generally distributed bunches of Stipa had produced about 13 inches of new growth, *Andropogon furcatus* 8 inches, *Sporobolus heterolepis* 5.5 inches, but Agropyron none. By August 15, only *Sporobolus asper* had recovered enough to fruit. The flower stalks in the widely spaced bunches were well over a meter tall.

Within the plots Agropyron and downy brome *(Bromus tectorum)* were the only grasses able to take advantage of the lessened competition correlated with the huge losses suffered by little bluestem, Koeleria, and Kentucky bluegrass and to a smaller degree by big bluestem, Canada bluegrass, *Panicum scribnerianum*, Stipa, and prairie dropseed. The large gain in number of plots occupied by Oxalis was less impressive than that of Lepidium because of the relative numbers of plants involved. Very large increases by the only annual grass, downy brome, failed to offset the smaller percentage decreases by perennials. Both annual and perennial forbs made distinct increases, the former gaining by about the same percentage as the ruderals[1] (Table 2).

Each meter quadrat was divided into 100 units, each one decimeter square, in order to permit accuracy in listing. In eight of the plots, one or more of the square decimeter units of observation were bare the first year. The total number of these bare units decreased from 78 to 57 in spite of the creation

[1] The term *ruderal* (weed) is used to mean an herb not originally a component of prairie vegetation.

of many new ones. The principal invaders of these areas were, in order of decreasing importance, catchfly *(Silene antirrhina)*, peppergrass *(Lepidium virginicum)*, seedlings of daisy fleabane, goat's-beard, and downy brome.

FIG. 6. Goat's-beard, an introduced weed, on the part of the low prairie dominated by needle grass and big bluestem.

TABLE 2. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT JAMAICA, NEBRASKA

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	1,334	1,869	+ 40.0	11	2	0
Andropogon furcatus	1,094	569	— 48.0	10	0	1
Andropogon scoparius	908	21	— 97.6	8	0	7
Bromus tectorum	244	863	+253.7	4	2	1
Carex	533	145	— 72.8	9	0	1
Koeleria cristata	830	5	— 99.4	4	0	3
Panicum scribnerianum	75	39	— 48.0	8	2	1
Poa compressa	216	133	— 38.4	4	0	0
Poa pratensis	6,412	2,428	— 62.1	10	1	2
Sporobolus heterolepis	72	50	— 30.5	2	0	0
Stipa spartea	574	300	— 47.7	4	0	1
NON-GRASSES						
Artemisia gnaphalodes	253	131	— 48.2	6	0	2
Aster multiflorus	334	685	+105.1	10	1	1
Erigeron ramosus	198	359	+ 81.3	6	2	1
Hedeoma hispida	76	129	+ 69.7	7	2	0
Lepidium virginicum	108	635	+487.9	9	3	0
Oxalis	24	37	+ 54.2	7	6	0
Rosa arkansana	13	9	— 30.8	4	0	1
Solidago glaberrima	102	113	+ 10.8	8	1	3
Tragopogon pratensis	177	287	+ 62.1	10	3	0

Only 16 unit areas were devoid of plants both years. The 41 newly bared areas were made so by the disappearance of 16 species, chief among which were bluegrass, daisy fleabane, aster, and little bluestem.

When the behavior of different ecological groups of species was studied, it was again seen that grasses suffered more than forbs, and perennials more than annuals (Table 3).

TABLE 3. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT JAMAICA, NEBRASKA

	Number of species	Number of Stems		Percentage of change	Number of plots	Species Per Plot	
		1936	1937			Average 1936	Percentage of change 1937
Grasses	19	15,564	9,103	— 41.5	13	5.92	— 15.5
Annual	1	244	863	+253.7	3	.15	+ 50.0
Perennial	18	15,320	8,240	— 46.2	13	5.77	— 17.3
Forbs	29	1,107	2,016	+ 82.1	12	4.46	+ 19.0
Annual	6	302	944	+212.5	8	.85	+100.0
Perennial	23	805	1,072	+ 33.1	12	3.62	0
Ruderals	5	570	1,824	+220.0	12	1.77	+ 21.4
Total	52	16,997	12,080	— 28.9	13	12.0	+ 2.5

On a per-plot basis, the number of kinds of annual forbs doubled but perennials made no change, while perennial grasses lost 17 percent and weeds gained 21 percent.

Selection was made of an area on low, level ground having a well developed wheat-grass sod surrounding an "island" of big bluestem. Dead and living bunches of prairie dropseed showed by their abundance that it had once been codominant here with big bluestem. Aster was present and prairie rose abundant, all within four square rods (Fig. 7). A moderately hard claypan was present at depths ranging from 14 to 21 inches in wheat grass territory but not in the big bluestem nor prairie dropseed. The results of infiltration experiments are shown in Figure 8 and soil moisture conditions in Table 1. The first inch of water required 23 minutes to enter the soil covered with wheat grass, but disappeared in the other types in 8 minutes or less, requiring only 1.1 minutes in bunches of prairie dropseed. The addition of each successive inch resulted in a lag in infiltration rate for at least one type. The soil in which aster was rooted absorbed the 4 inches in 1.6, 2.9, 3.3, and 4.4 minutes respectively, while the rate for big bluestem was 8.0 and 20.5 for the third and fourth inches. Soil occupied by Agropyron did not absorb the first half of the third inch even after 16.5 hours.

The composite of shallow random soil samples obtained in August, 1937, yielded seedlings of 22 species during 5 months in the greenhouse. Annuals comprised 82 percent of the species and 86 percent of the plants. The 10

ruderals present provided 0.4 of the seedlings. Catchfly was the most abundant species.

CRETE AND LINCOLN PRAIRIES

These prairies are treated together because of their proximity and similarity as to vegetation, soil, and topography. The Crete prairie of 60 acres

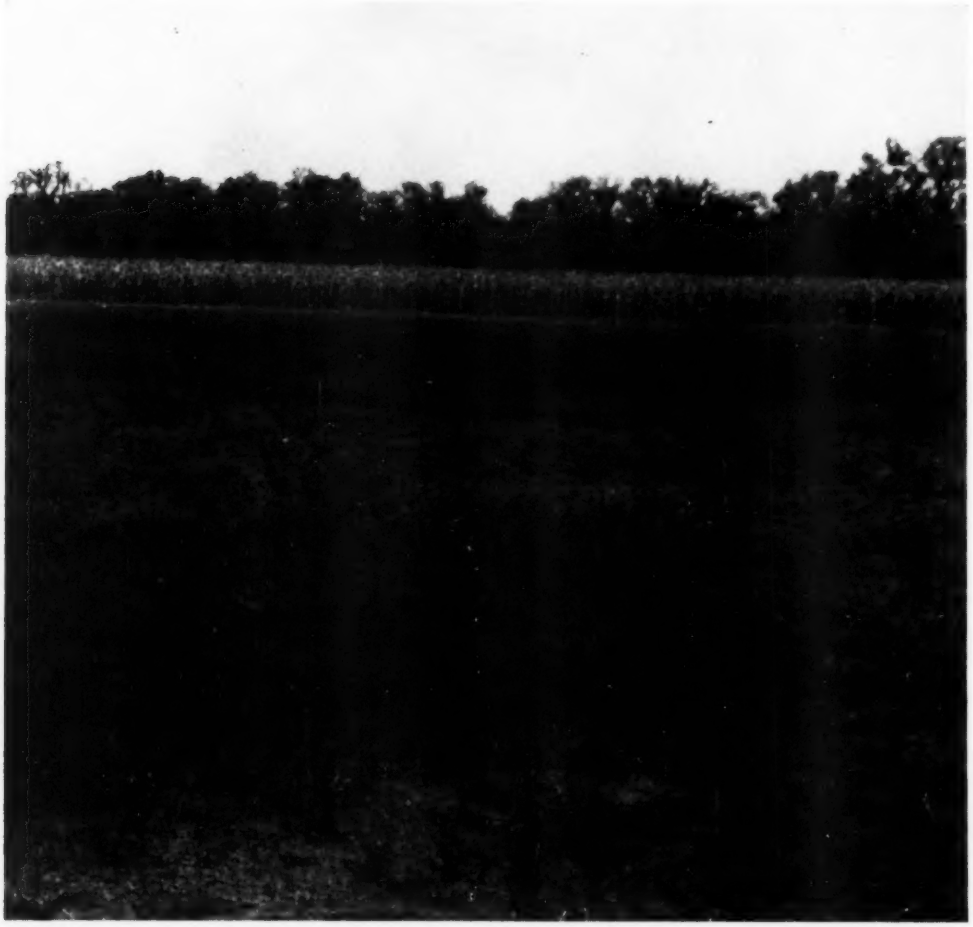

FIG. 7. The areas of wheat grass and bluestem where infiltration rates were measured 2 months after mowing. The dark area is big bluestem, the light area, wheat grass.

is eight miles northeast of Crete, Nebraska, and is one mile west of the prairie of the same name described by Weaver and Albertson (1936). The Lincoln prairie lies 8.5 miles northwest of the University of Nebraska. It includes nearly a section (640 acres) but this study was restricted to approximately 200 acres in the southeast corner.

Both tracts consist of flat-topped hills separated by grassy swales and wooded ravines. The soil is Carrington silt loam of glacial derivation. It is dark, granular, friable, and without lime in the first foot but harder, yellow, and speckled with grains of lime at a depth of three feet. Pure veins of lime

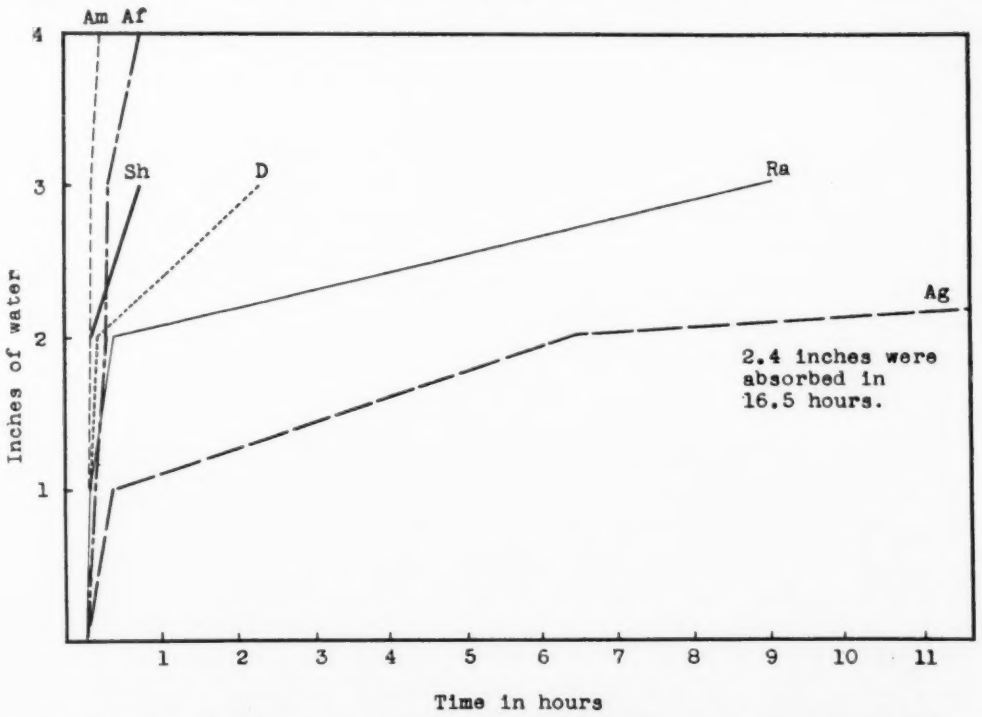

FIG. 8. Rate of infiltration of water into the soil in 6 types of vegetation at Jamaica, Nebraska; aster (Am), big bluestem (Af), prairie dropseed (Sh), dead crowns of prairie dropseed (D), prairie rose (Ra), and western wheat grass (Ag).

are occasionally encountered at four feet and glacial pebbles at all depths. High uniformity in texture is suggested by the narrow range in hygroscopic coefficients to a depth of 15 feet (Table 4). However, very sandy areas are

TABLE 4. PERCENTAGE OF AVAILABLE SOIL MOISTURE OF NEARLY LEVEL UPLAND (ANDROPOGONS), LOWLAND (SPARTINA), AND A XERIC SLOPE (BOUTELOUA-SPOROBOLUS)

	Crete Prairie						Lincoln Prairie			
	Upland			Lowland			Southwest Exposure			
Depth in feet	Hygroscopic coefficient	August 10 1936	August 10 1937	Hygroscopic coefficient	August 10 1936	August 10 1937	Hygroscopic coefficient	July 30 1936	June 7 1937	August 5 1937
0-.5 ..	10.8	1.7	0.0	11.2	0.7	0.7	7.3	—2.4	—0.4	0.2
.5-1 ..	12.2	1.6	0.3	11.0	0.1	1.5	7.6	—0.8	5.8	1.5
1-2 ..	13.3	0.7	0.9	9.6	3.0	3.8	7.4	—1.5	4.0	0.0
2-3 ..	11.5	0.8	2.7	11.0	3.6	2.5	5.2	0.0	1.6	0.1
3-4 ..	10.6	3.6	2.3	11.4	4.6	3.6	4.6	0.1	0.4	—0.1
4-5 ..	11.9	3.2	1.2	10.9	5.5	4.8				
5-6 ..	11.8	4.2	3.5	11.1	7.7	5.8				
6-7 ..	11.3	6.4	5.1	11.7	10.8	4.8				
7-8 ..	11.4	7.1	3.9	11.8	12.3	9.4				
8-9 ..	11.8	8.3	3.3	11.4	12.2	13.1				
9-10 ..	11.8	9.5	8.0	13.8	13.0	10.8				
10-11 ..	10.0	8.6	...	10.5	13.7					
11-12 ..	9.7	8.2	...	11.7	13.6					
12-13 ..	10.8	9.8	...	11.9	12.9					
13-14 ..	12.2	9.8	...	12.0	12.9					
14-15 ..	12.8	9.7	...	11.9	12.7					

not infrequent. Enough fine material is present to give this soil a high water-holding capacity, but it is easily permeable to both water and roots.

The soil and vegetation of the Lincoln prairie were fully described before the drought (Steiger 1930). *Andropogon scoparius* was dominant on the upland and occurred most constantly in random upland plots, followed by *Bouteloua gracilis, Sporobolus heterolepis, Poa pratensis, Andropogon furcatus,* and *Boutelou curtipendula.* The most abundant upland forbs, in order of decreasing importance, were *Amorpha canescens,* prairie cat's foot *(Antennaria campestris), Solidago glaberrima,* and wild alfalfa *(Psoralea floribunda). Aster multiflorus* ranked eighth in 1928. The exact structure of the Crete prairie before the drought is not known.

FIG. 9. One of the many upland areas left bare by the death of *Sporobolus heterolepis* following the drought of 1936.

Meteorological data presented for the Jamaica prairie may be considered as approximate, also, for these prairies (Figs. 4 and 5).

These areas were studied each year in late July and early August. The vegetation was extremely dry in 1936. The more mesic grasses were so brittle that stems readily broke off underfoot. Many large cracks were present, especially in bluegrass sod, and excessive disturbance by rodents was apparent. Drought injury in 1934, as judged from the number of dead crowns present, was less than on prairies farther south and west. Invasion by wheat grass and downy brome, and increase in abundance of aster were also comparatively less. The most abundant grasses were big bluestem, little bluestem, and prairie dropseed. The last appeared to have come through the

drought of 1934 nearly unscathed. Needle grass and side-oats grama were common and of general distribution. Many well established patches of smooth brome grass *(Bromus inermis)* were present at Crete where the yield in 1936 was scarcely one-half ton of hay per acre.

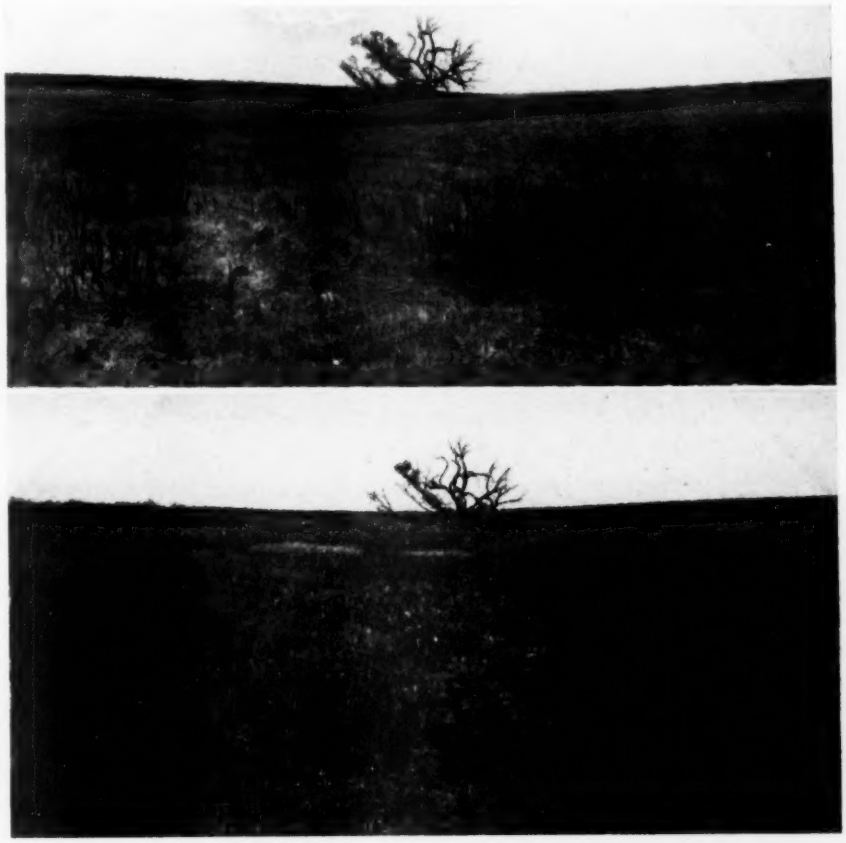

FIG. 10. A slough-grass ravine at Crete in 1936 (above) and 1937 (below). Two crops of hay were produced by Spartina the first year but the ravines were too weedy for mowing in 1937. Note the progressive injury to the willow.

Only the most deeply rooted upland forbs, for example Amorpha and Aster, were not badly dried. The behavior of Amorpha in folding it leaves daily indicated that the moisture-supplying capacity of the subsoil was quite low (Table 4). Scarcely any moisture was available in the Lincoln prairie to root systems penetrating less than four feet. Antennaria, which failed to recover when watered at a depth of 2.5 feet (Weaver *et al.* 1935), was infrequent on these prairies and absent on others. Aster had advanced from eighth position to replace Amorpha as the most important forb.

Abundance of other important forbs in 1936 and 1937 was as follows: Amorpha, 3-3; Erigeron, 2-2; Hedeoma, 4-3; *Helianthus rigidus*, 2-3; and *Solidago glaberrima*, 3-3.

Seven plots containing 40 species were established at the Lincoln prairie and eleven containing 52 species at Crete. A census was taken each year. In 1937 certain vegetational changes were obvious owing to the drought of the previous year. Much prairie dropseed and Kentucky bluegrass had been killed, leaving numerous areas protected from erosion only by dead crowns and rhizomes (Fig. 9). These and other areas were rapidly being invaded by Agropyron and Aster, in some instances nearly to the bottoms of ravines. The rank growth of Aster and other weedy species, coupled with the sparseness of perennial grasses, reduced the value of the hay so that most of each prairie was left unmowed (Fig. 10). The 75 percent foliage cover of the hilltops consisted largely of seedlings of Erigeron, Senecio, and Tragopogon.

Big bluestem had merely grown less dense in the 16 plots it occupied, but little bluestem had disappeared from four plots while appearing in two new ones in 1937 (Table 5). The loss by bluegrass was due in part to severe injury by grasshoppers. Other perennial grasses which lost ground were sideoats grama, June grass, and the carices. Needle grass and switch grass showed small gains, but wheat grass increased over 40 percent. Comparable increases were shown only by aster, daisy fleabane, and peppergrass. These three species are representative of perennial forbs, annual forbs, and ruderals, the abundance of which is shown in Table 6. Perennial grasses alone, of the five groups, were reduced by the drought.

The number of species per plot (13.7) was the same on both prairies in 1936.

TABLE 5. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937. CRETE AND LINCOLN PRAIRIES

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	705	997	+ 41.4	7	0	1
Andropogon furcatus	1,536	1,057	— 31.2	16	0	0
Andropogon scoparius	1,383	131	— 90.5	13	2	4
Bouteloua curtipendula	913	789	— 13.6	11	1	0
Carex	949	346	— 63.5	14	0	4
Koeleria cristata	578	177	— 69.4	11	0	3
Panicum virgatum	288	300	+ 4.2	8	2	4
Poa pratensis	2,066	1,940	— 6.1	14	0	5
Sporobolus heterolepis	1,291	460	— 64.4	12	0	4
Stipa spartea	148	163	+ 10.1	11	0	3
NON-GRASSES						
Amorpha canescens	50	44	— 12.0	8	0	1
Aster multiflorus	717	875	+ 22.0	15	1	0
Erigeron ramosus	164	361	+120.1	14	3	1
Helianthus rigidus	69	40	— 42.0	7	0	2
Lepidium virginicum	68	1,084	+1,494.1	10	2	1
Silphium integrifolium	462	392	— 15.1	1	0	0
Solidago glaberrima	30	26	— 13.3	10	4	1

TABLE 6. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT CRETE AND LINCOLN PRAIRIES

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	24	10,457	7,750	− 25.8	17
Annual	4	53	82	+ 54.7	8
Perennial	20	10,404	7,668	− 26.3	17
Forbs	26	1,687	2,008	+ 19.0	18
Annual	6	173	437	+152.6	15
Perennial	20	1,514	1,571	+ 3.8	18
Ruderals	11	179	1,217	+579.9	14
Total	59	12,301	10,915	− 11.3	18

Study of the 88 units of observation that were bare the first year showed that 74 were invaded in 1937, chiefly by Erigeron and Lepidium. Death of Poa, *Andropogon furcatus, Sporobolus heterolepis,* and Erigeron resulted in most of the 106 new bare units.

Big bluestem ranked first and aster third in percentage frequency in 85 random plots in both 1936 and 1937. The first year bluegrass was second with needle grass and lead plant fourth and fifth. Side-oats grama was second in frequency, peppergrass fourth, and daisy fleabane fifth in 1937. Little bluestem, which was most frequent in 1928, occurred in 30 and 9 percent of the plots during the two years, respectively.

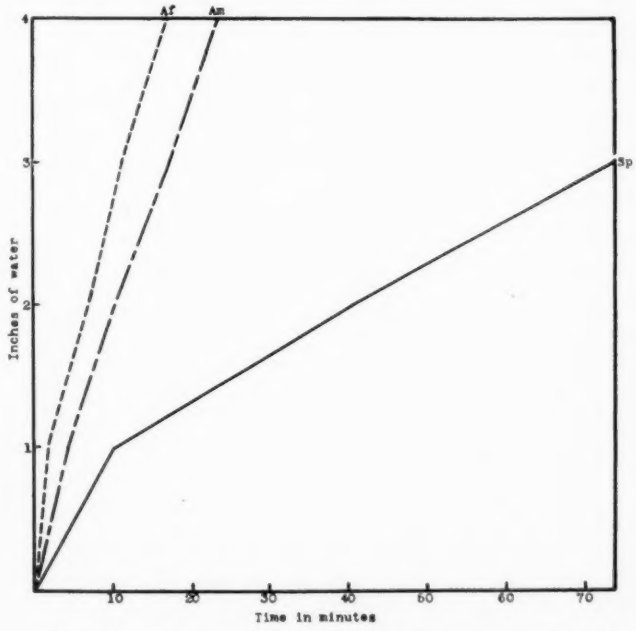

FIG. 11. Rate of infiltration of water into the soil in 3 types of vegetation at Crete, Nebraska; big bluestem (Af), aster (Am), and slough grass (Sp).

Perennial forbs were slightly shorter in 1937, in spite of higher precipitation than in 1936, but perennial grasses were 40 to 50 percent higher.

The rates of infiltration of water in three types of vegetation were measured at the end of the growing season in 1937. As usual, sod of big bluestem absorbed most readily. The time required increased from 2 minutes for the first inch of water to 5.4 for the fourth. Seven minutes longer were required in aster sod, and in slough grass only 3 inches were

absorbed in 74 minutes (Fig. 11). Range in rate of absorption in the 4 cylinders was rather large, especially in bluestem. For the three types of vegetation the average rate of infiltration was 2.8 times as rapid in the fastest as in the slowest cylinder.

A composite of random samples of surface soil was made up in August, 1937, from the Crete prairie. Under greenhouse care during 5 months, this sample yielded seedlings of 24 species. Only one fifth of the species and 4 percent of the plants were perennials. Ruderals constituted one fourth of the seedlings, but Kentucky bluegrass was the most abundant species.

HEBRON PRAIRIE

The Hebron prairie occupies most of a rolling upland tract of 30 acres two miles south of that city (Fig. 1). It consists of a low divide and parts of 3 shallow ravines, the broader of which is in cultivation and contains the only level land on the tract. Soils of two series are represented. The northeast one fourth is Shelby fine sandy loam. Although gravel is to be seen on the surface, the first foot is a fine sandy loam which gives way at a depth of 1 to 2 feet to light colored, gravelly subsoil. The remainder of the prairie is Nuckolls silt loam, a soil of much greater water-holding capacity. No carbonates occur to a depth of 4 feet.

In 1931, this prairie was dominated by *Andropogon scoparius* of the xeric bunch type intermingling with *A. furcatus* on the upland, and on dry slopes with a high percentage of *Bouteloua curtipendula* and *B. gracilis*. Koeleria was abundant, Stipa and Buchloe rare. Abundance of forbs in 1931 is shown in Table 7.

TABLE 7. RELATIVE ABUNDANCE OF THE CHIEF FORBS AT HEBRON, NEBRASKA. THE FIGURE 1 MEANS VERY ABUNDANT, 2 ABUNDANT, 3 COMMON, 4 INFREQUENT, 5 RARE, AND 0 NOT SEEN.

Species	1931	1936	1937
Amorpha canescens	1	3	3
Artemisia gnaphalodes	3	3	4
Aster multiflorus	1	1	2
Erigeron ramosus	1	1	3
Hedeoma hispida	4	0	3
Liatris punctata	4	4	3
Linum sulcatum	5	5	3
Opuntia humifusa	0	3	4
Plantago purshii	5	4	2
Psoralea argophylla	3	5	0
Senecio plattensis	3	0	0
Solidago glaberrima	3	3	3

The summer of 1936 at Hebron was characterized by maximum temperatures of 108°, 111°, and 109° F. for June, July, and August, respectively. From May to August, inclusive, the greatest rainfall in one day for each of the consecutive months was 0.95, 1.3, 1.1, and 0.9 inches. During that time two drought periods occurred. None of the 39 days from June 18 to July 26 received more than 0.08 inch of rain, and in August, 20 consecutive days

passed with no effective rain. Precipitation for the year was 12.87 inches. All except two months, January and September, received less than normal rainfall while mean monthly temperatures were much higher in summer and lower than normal in winter. The year 1935 had 10.5 inches above normal precipitation, while 1934 and 1936 each had about equally low rainfall (Fig. 12). That available moisture was largely depleted in the upper 3 feet is shown in Table 8.

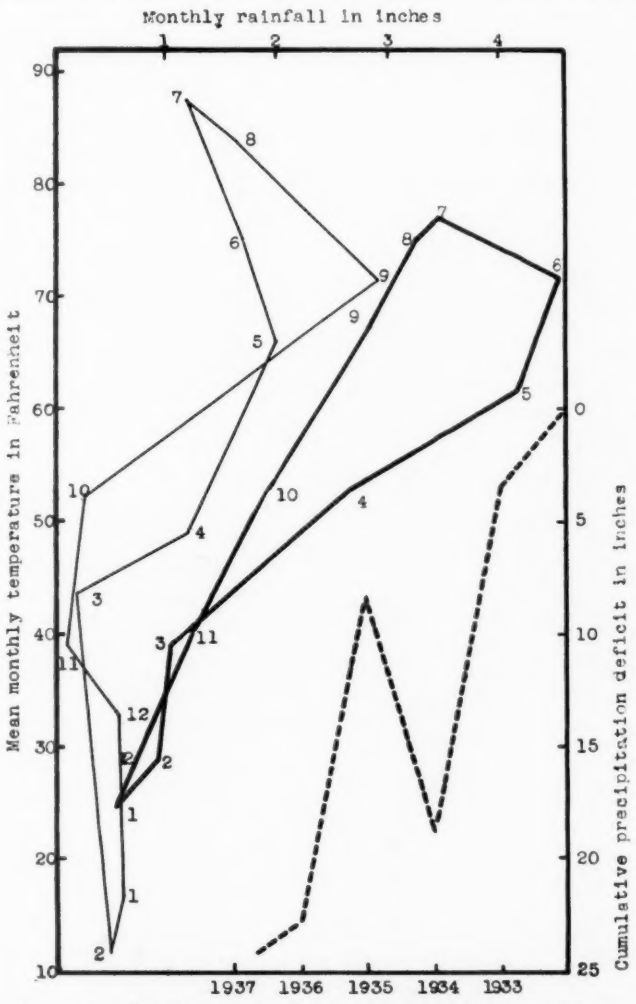

FIG. 12. Hythergraph of mean monthly temperature and rainfall for 1936 (light line) and for a 35-year period (heavy line) at Hebron, Nebraska. Broken line shows cumulative precipitation deficit from January, 1933, to August, 1937.

Burning had been used here as a method of weed control. June grass was usually abundant over most of the prairie, both as mature plants fruiting at heights of 4 to 18 inches, and as seedlings. Locally it provided a basal cover of 5 to 10 percent but was most conspicuous along cracks on poorly covered ridges.

Wheat grass was limited to two sharply defined alternes, both coinciding with recent deposits of dust from cultivated fields on the north and south (Fig. 13). The dust varied in depth from over an inch at the center to one-fourth inch at the edge where the wheat grass bordered bluestems and grama grasses. The scattered tufts of little bluestem were nearly always sheltered by big bluestem and appeared to be much more vigorous than the latter.

Where the heat had been the greatest on burned spots, only blue grama had survived.

Thirteen permanent plots, enclosing 11 square meters and including 48 of the 63 species observed on the prairie, were located in different types of

TABLE 8. PERCENTAGE OF AVAILABLE SOIL MOISTURE OF UPLAND ON GENTLE NORTHWEST SLOPE AT HEBRON, NEBRASKA

Depth in feet	Hygroscopic coefficient	1936	1937	
		July 22	June 7	July 22
0-.5	7.0	-2.7	22.0	5.0
.5-1	7.4	-0.5	10.7	2.9
1-2	12.6	0.2	7.9	0.0
2-3	12.0	-2.6	3.1	1.9

vegetation. A census was taken in 1936 and again in 1937 and heights of species in each plot were recorded. In addition, a record was made of the species found in each of 33 temporary plots.

On August 4, 8 days after a 1.1-inch rain, each tuft of little bluestem had new leaves among the dead ones while the 9 inches of new growth of big bluestem upheld dead tips 3 to 5 inches long.

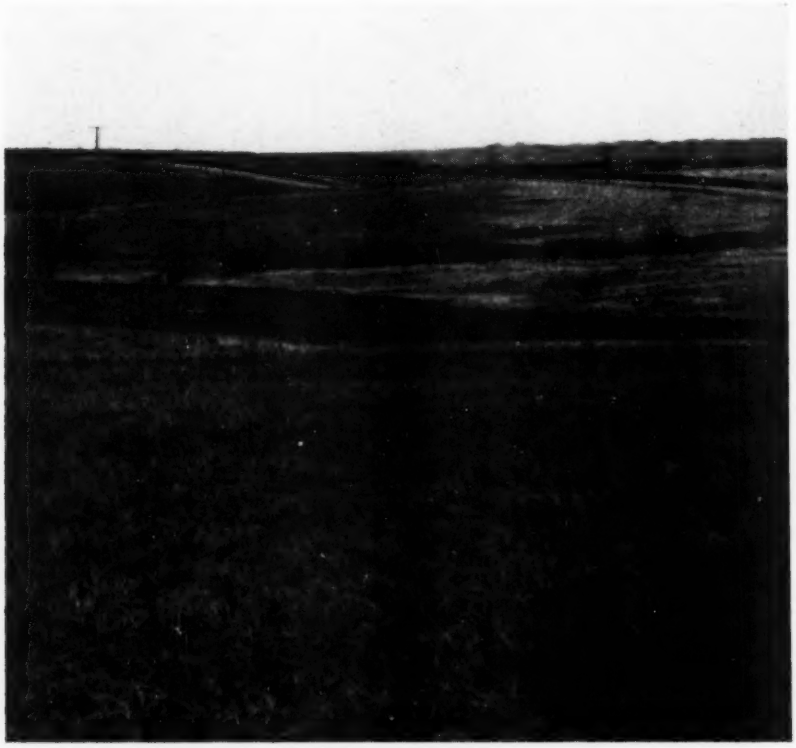

FIG. 13. Wheat-grass alternes established on wind-deposited dust (white). Agropyron was reduced in density but not in extent in 1937.

During the first 6 months of 1937, the mean monthly rainfall was normal while temperatures averaged 2.6° F. below normal. The longest drought period, 17 days, ended with an inch of rain on July 3. Six more showers totaling 2 inches occurred before the date of study. This precipitation was reflected by the soil moisture content (Table 8) and especially by the condition of the vegetation, which was obviously taller and weedier. Downy

brome was distributed over the whole prairie, whereas Agropyron had spread but little, becoming less dense in its former territory. Elymus had invaded the upland and was established in many small patches. Koeleria and sand dropseed were abundant, but Poa and Eragrostis were rare (Fig. 14). Among the forbs yellow flax *(Linum sulcatum)* and Hedeoma were much more abundant (Table 7).

FIG. 14. June grass *(Koeleria cristata)* in the Hebron prairie where burning was practiced.

Analysis of data from the permanent plots, summarized in Tables 9 and 10, shows that some of the perennial grasses, big bluestem, Poa, Koeleria, *Panicum scribnerianum,* and *P. wilcoxianum* lost 11 to 93 percent of the number of stems present in 1936. Others, such as Agropyron, little bluestem, species of Carex, blue grama, and side-oats grama made gains of 1 to 65 percent, but the net loss in abundance of perennial grasses was 20 percent.

Annual grasses, that is Hordeum, Bromus, and Festuca, were abundant in 1937 but not in 1936. Stems of the last were so numerous that increase was calculated on the basis of the number of square decimeters occupied. Annual forbs, for example Plantago and Linum, were consistent in making enormous gains which for the 7 species averaged 674 percent. Perennial forbs, on the other hand, were inconsistent. Amorpha made a small gain in abundance, Aster decreased 25 percent, and Solidago increased 1.5 times, largely due to the presence of seedlings. The average gain of 14 species of these deep-rooted forbs was 19 percent.

Other ruderals than downy brome made large gains as well. Peppergrass led this group of six species with its gain of nearly 90 fold. The average gain of all species in the 13 plots was 26 percent. Moreover, the prairie as a whole appeared to have a much denser cover.

The average number of species per plot was 15.7 in 1937, or 17 percent greater than the previous year. Considered similarly, species of perennial grasses were 22 percent fewer, annual grasses 42 percent more numerous, annual forbs and ruderals each 150 percent more abundant, but perennial forbs were unchanged.

TABLE 9. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES IN PERMANENT PLOTS AT HEBRON, NEBRASKA, NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937; ALSO THE PERCENTAGE OF TEMPORARY PLOTS IN WHICH SPECIES OCCURRED IN 1936 AND 1937

Species	Number of Stems		Percentage of change	Number of Plots			Percentage Occurrence In Temporary Plots	
	1936	1937		Total	Invaded	Vacated	1936	1937
GRASSES								
Agropyron smithii	900	908	+ 0.9	4	0	1	16	9
Andropogon furcatus	2,035	1,806	— 11.2	10	0	0	82	81
Andropogon scoparius	574	660	+ 15.0	7	0	1	26	27
Bouteloua curtipendula	364	600	+ 64.8	9	0	2	24	45
Bouteloua gracilis	703	785	+ 11.7	6	0	0	44	57
Bromus tectorum	63	872	+1,284.1	7	3	0	2	30
Carex	318	353	+ 11.0	9	0	2	36	39
Festuca octoflora	(485)*	(833)*	+ 71.8	11	2	0	36	87
Koeleria cristata	2,082	940	— 54.9	10	0	1	66	54
Panicum scribnerianum	61	35	— 42.6	8	1	2	12	18
Panicum wilcoxianum	39	3	— 92.3	7	1	5	6	3
Poa pratensis	745	52	— 93.0	5	0	3	12	3
NON-GRASSES								
Amorpha canescens	85	94	+ 10.6	8	0	1	66	57
Aster multiflorus	273	205	— 24.9	8	0	1	48	48
Erigeron ramosus	380	945	+152.1	11	0	1	72	78
Hedeoma hispida	0	851	+	11	11	0	0	75
Lepidium virginicum	3	271	+8,933.3	8	6	0	4	33
Linum sulcatum	0	320	+	7	7	0	2	57
Plantago purshii	45	1,144	+2,442.2	5	1	0	22	45
Solidago glaberrima	20	50	+150.0	6	1	1	28	21

*Number of square decimeter units in which species occurred.

TABLE 10. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT HEBRON, NEBRASKA

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	22	8,192	7,410	— 9.5	13
Annual	2	100	914	+814.0	8
	1	(488)*	(849)*	+ 74.0	11
Perennial	19	8,092	6,496	— 19.7	13
Forbs	21	989	3,958	+300.2	11
Annual	7	425	3,289	+673.9	11
Perennial	14	564	670	+ 18.8	10
Ruderals	6	112	1,164	+939.3	10
Total	48	9,230	11,661	+ 26.3	13

*Number of square decimeter units in which species occurred.

When first quadrated, 35 of the square decimeter areas were bare but not one in 1937. This increase in general density was due to invasion by 21 species, of which 7 were perennial and 3 annual grasses; 4 were perennial forbs, and the rest annual forbs and weeds. Festuca, Hedeoma, Erigeron, and Plantago were the chief invaders.

The vegetation was much taller (58 percent) in 1937, the average height being 11 inches. Perennial grasses were 73 percent and annual grasses 214 percent taller. Perennial forbs were 33 percent and ruderals 125 percent taller. These increases in stature were related to the difference in available moisture (Table 8).

Since percentage occurrence in temporary, random plots may be considered as indicative of the distribution of individual species, data are given in Table 9 for the 20 species that were also most prominent in the permanent plots. Gains and losses in the latter are in agreement with increased and restricted distribution as found in the temporary plots for all but 4 species. For these the disagreement is small or explainable by the fact that the species are restricted to a few alternes.

BELLEVILLE PRAIRIE

Four miles east of Belleville, Kansas, there is a well-drained, north-sloping, upland prairie of about 15 acres.

The pervious, black loam soil is derived from soft limestone parent material which occasionally lies within 3 feet of the surface on both high and low ground. Below one foot, the black topsoil gives way to light brown, then to yellow, less pervious, clayey subsoil. Lime content varies from zero in the first 6 inches to nearly pure limestone at 4 feet. Soil reaction in the first 6 inches varied from pH 5.4 on the upland to pH 7.3 in a wheat-grass hollow, and to pH 7.8 at a depth of 2 to 3 feet. Salt content at this depth ranged from 4 to 388 p.p.m., being less at shallow depths, and highest where wheat grass was dominant.

The vegetation in 1931 was characterized by co-dominance of big bluestem with both sod and bunch types of little bluestem on the upland, and with nodding wild rye in the ravines. Wheat grass was limited to a steep-sided hollow on the east. Numerous alternes of buffalo grass and blue grama, both pure and mixed, occurred on the upland as did the generally distributed side-oats grama, June grass, and prairie dropseed. Cactus, plantain, and rough pennyroyal were present.

Although 1936 was the driest year on record for Kansas, the rainfall deficiency in the vicinity of Belleville was only 48 percent as great as in 1934. The maximum temperature attained in 1936 (114° F.) was 1 degree less than the 1934 maximum. Only 3 months of 1936 had adequate rainfall, while winter temperatures were below and summer temperatures above normal (Fig. 15).

On June 29, available soil moisture was present to a depth of 4 feet in the blue-grama alternes but was exhausted between 2 and 4 feet in the big-bluestem type a few feet distant. However, more water was available in the first foot in the latter (Table 11).

Late in June, the vegetation of ravines and protected slopes was thriving, but that of the upland was dwarfed and the cover quite open. The dominants were wheat grass and big bluestem, the former being densest on deposits of dust from adjacent fields. Little bluestem was represented by generally distributed wisps of 2 to 6 stems on the edges of otherwise dead bunches. It was exceeded in abundance by both side-oats grama and six-weeks fescue. Both buffalo grass and blue grama formed nearly pure alternes on ridges and exposed slopes. June grass and *Panicum scribnerianum* were common, but Kentucky bluegrass was rare. Downy brome and plantain were locally abundant as colonists in bared areas. Abundance of other forbs was as follows, the rankings being for 1936 and 1937, respectively: Amorpha, 2-2; Artemisia, 2-4; Aster, 1-3; Erigeron, 3-2; Hedeoma, 3-1; Liatris, 3-4; sensitive-brier *(Morongia uncinata)*, 3-3; Opuntia, 4-3; and Solidago, 4-4.

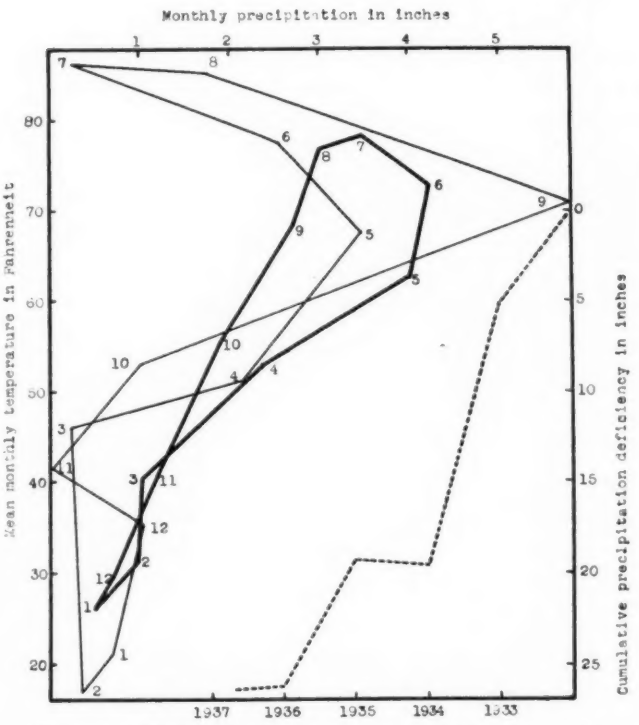

FIG. 15. Hythergraph of mean monthly temperature and rainfall for 1936 (light line) and for a 33-year period (heavy line) at Belleville, Kansas. Numbers 1 to 12 represent months. Broken line shows cumulative precipitation deficit from January 1, 1933, to August 31, 1937.

TABLE 11. PERCENTAGE OF AVAILABLE SOIL MOISTURE IN TWO UPLAND TYPES OF VEGETATION AT BELLEVILLE, KANSAS

Depth in feet	Hygroscopic coefficient	*Bouteloua gracilis*		*Andropogon furcatus*
		June 29 1936	June 7 1937	June 29 1936
0-1	12.1	6.5	8.6	16.3
1-2	13.6	0.3	3.9	0.3
2-3	13.2	1.6	0.3	— 0.9
3-4	13.0	0.5	0.8	— 0.3

A census taken in the 11 permanent plots the last week in June in both 1936 and 1937 revealed that they contained 54 of the 78 species observed.

Precipitation for the first 6 months of 1937 was 0.3 inch below normal, and soil moisture below 2 feet had not been increased (Table 11). Temperature during the summer averaged 4° F. above normal. In spite of apparently better growing conditions in 1937, the vegetation was again badly dwarfed. Perennial grasses were slightly taller but the average height of the vegetation (10 inches) was the same as the previous year. Because of the abundance of annuals, the cover appeared denser than the year before.

Other obvious changes were a further large reduction in density of little bluestem and such an increase in wheat grass that the dominance of the depleted big bluestem was challenged.

Switch grass *(Panicum virgatum)*, blue grama, June grass, and the bluestems sustained losses ranging from 12 to 95 percent. Despite moderate gains by side-oats grama, wheat grass, nodding wild rye, and dropseed, the net result was a reduction of 17 percent in perennial grasses (Tables 12 and 13).

Big bluestem formed numerous large, dense bunches in the ravine in 1936. The following year these were open and invaded by bluegrass, dropseed, and nodding wild rye. This apparently represents the first step in changing from the bunch to the sod form which is prevalent in drier habitats. Perennial forbs, with such losses as 70 percent for Aster and 90 percent for Artemisia,

TABLE 12. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, WITH TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT BELLEVILLE, KANSAS

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
Grasses						
Agropyron smithii	887	1,047	+ 18.0	7	1	0
Andropogon furcatus	1,822	1,037	— 43.1	10	0	0
Andropogon scoparius	178	9	— 94.9	4	0	3
Bouteloua curtipendula	1,146	1,300	+ 13.4	10	0	1
Bouteloua gracilis	7.62*	5.90*	— 22.6	8	1	0
Buchloe dactyloides	0.53*	0.53*	0	2	1	0
Carex	182	181	— 0.5	7	1	1
Elymus canadensis	23	31	+ 34.8	3	0	0
Koeleria cristata	394	279	— 29.2	9	0	2
Panicum virgatum	132	116	— 12.1	3	0	0
Sporobolus asper	362	585	+ 61.6	7	0	1
Non-Grasses						
Amorpha canescens	33	43	+ 30.3	4	1	0
Androsace occidentalis	0	472	+	7	7	0
Artemisia gnaphalodes	178	18	— 89.9	4	0	1
Aster multiflorus	390	125	— 67.9	6	1	1
Erigeron ramosus	59	543	+820.3	10	4	0
Hedeoma hispida	62	1,862	+2,903.2	9	0	0
Lepidium virginicum	31	1,165	+3,658.1	9	4	0
Plantago purshii	355	4,121	+1,060.8	7	0	0
Spermolepis patens	0	163	+	5	5	0

*Estimated cover in percent.

showed an average decrease of 67 per cent, but annual grasses, forbs and weeds became 8 to 36 times more abundant (Fig. 16).

The total number of species per plot increased from 13.5 to 16.9, which was the highest number and largest increase recorded for any prairie. This was due to invasion by annuals. While there were 4 percent fewer species of perennial grasses and 7 percent fewer species of perennial forbs, annual grasses had increased 24 percent, weeds and annual forbs 100 percent.

FIG. 16. *Plantago purshii* at Belleville. This early annual overtopped the short grasses in June, 1937.

Dissemination of annuals was such that bare units of observation were rare in 1937, although 29 were present in 1936. The chief invaders were Festuca, Lepidium, Hedeoma, Erigeron, and Spermolepis (all annuals).

The many clearly defined alternes afforded an opportunity to study the influence of different vegetation on absorption. The rate of infiltration of 4 inches of water was measured in 5 types. The time required for absorption ranged from 34.5 minutes in big bluestem on the upland to 47.4 minutes in the wheat-grass hollow. Soil permeated by the fine, fibrous roots of buffalo grass absorbed the water in 35 minutes, which was 6 minutes less than re-

TABLE 13. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT BELLEVILLE, KANSAS

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	23	10,497	10,422	— 0.7	11
Annual	3	361	1,992	+ 451.8	10
Perennial	20	10,136	8,430	— 16.8	11
Forbs	27	1,152	7,452	+ 546.9	10
Annual	9	476	7,228	+ 1,418.1	10
Perennial	18	676	224	— 66.9	10
Ruderals	5	237	2,112	+ 791.1	10
Total	54	11,683	19,074	+ 63.3	11

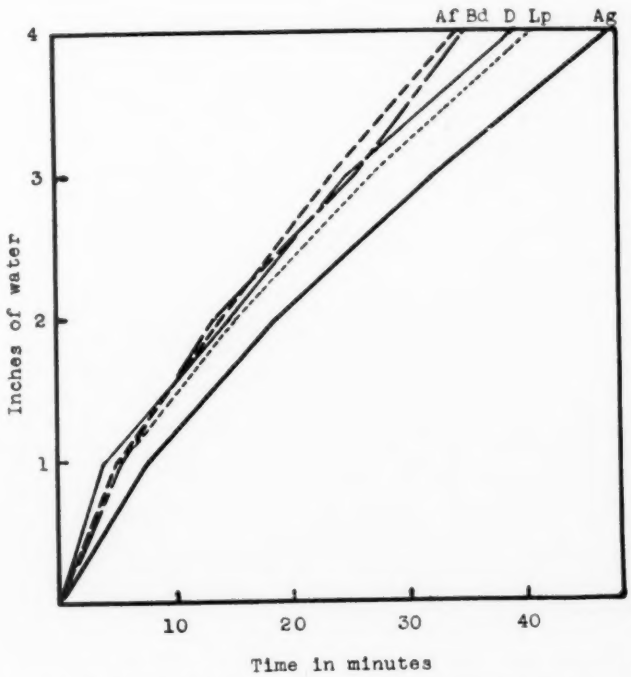

FIG. 17. Rate of infiltration of water into the soil in 5 types of vegetation at Belleville, Kansas; big bluestem (Af), buffalo grass (Bd), dead crowns of grass (D), blazing star (Lp), and wheat grass (Ag).

quired by soil occupied by a large taproot of blazing star. Soil covered only by crowns of dead grass absorbed the first inch in 4 minutes, but the total time was only a minute less than for blazing star (Fig. 17).

CARLETON PRAIRIE

A slightly rolling, typical upland bluestem prairie of 35 acres lies three miles southeast of Carleton, Nebraska. Its surface gives the impression of being slightly warped as the north part slopes to the east and the south to the west with a shallow swale draining diagonally eastward across the center. An old road, now seldom used, crosses the prairie from northwest to southeast and acts as a source of migrules of weedy annuals. The soil is all Crete silt loam. The topsoil is dark brown to black and coarsely granular. Lime is generally present at a depth of 2 to 3 feet and the soil is brown to light brown, hard and rather impervious at this depth. In the swale in the wheatgrass type a definite claypan is present, beginning at 9 to 12 inches and extending to depths of 26 to 30 inches. Over the remainder of the prairie this layer is present but more pervious and less superficial. Greater differences in acidity occurred between the depths of 6 inches and 3 feet (pH 4.5 to 7.4) than between samples from the upper 6 inches on different parts of the prairie (pH 4.5 to 5.7). No correlation was found between vegetation type and pH number.

Before the drought this prairie was dominated by the sod form of little bluestem except in the swales where this dominance was shared with big bluestem and wheat grass. That these swales once supported a more mesic vegetation is shown by the presence of relict switch grass, spike-rush *(Eleocharis acuminata)*, and clover fern *(Marsilia vestita)*. Several small alternes of blue grama and buffalo grass and one of needle grass were found. June grass was frequent but not abundant, and Kentucky bluegrass was locally abundant. Daisy fleabane, aster, poppy mallow, and lead plant were the most

abundant forbs. The relative abundance of these and other species is shown in Table 14.

Four days spent on this prairie in the middle of July, 1936, served to impress one with the severity of physical and biotic factors so extreme that even native vegetation could not endure them uninjured. Daily maximum temperatures ranging from 104 to 111° F. accompanied by relative humidities of 19 to 24 percent, continuous strong winds, glaring sunlight, and subnormal precipitation combined to make the grasses crackle underfoot like wheat stubble. Only prairie false boneset *(Kuhnia glutinosa)* and blazing star appeared unhampered by drought, and they were borne down and partly eaten by hordes of grasshoppers. Amorpha folded its leaves during the day and opened them only slightly by sunrise although the nights were cool and relatively calm. Foliage of all other plants was partly or entirely dead. Both bluestems appeared in all stages of perishing. Buffalo-grass foliage, including stolons as much as 16 inches long, was bleached and apparently lifeless. Bunches of blue grama, some a foot in diameter, seemed entirely dead.

Despite the excess supply of moisture in 1935, which resulted in a fair crop of hay, the subsoil moisture supply was greatly depleted (Table 17). The eastern half of the prairie was mowed in July, 1935, a month earlier than the western half. An economy of soil moisture was thus effected during a period which was too rigorous to permit growth. This, coupled with

TABLE 14. VARIATION IN ABUNDANCE AND FREQUENCY OF MOST IMPORTANT SPECIES AT CARLETON, NEBRASKA

Species	Relative Abundance			Temporary Plots Percentage Occurrence	
	1931	1936	1937	1936	1937
GRASSES					
Agropyron smithii	3	1	1	76	93
Andropogon furcatus	2	2	2	61	42
Andropogon scoparius	1	4	3	15	0
Bouteloua curtipendula	..	2	1	66	84
Bouteloua gracilis	3	2	3	20	21
Bromus tectorum	..	4	2	10	21
Buchloe dactyloides	4	3	4	2	0
Carex	4	3	3	57	39
Festuca octoflora	3	1	1	71	93
Koeleria cristata	2	4	4	42	9
Poa pratensis	3	3	3	25	12
Sporobolus asper	5	4	3	19	3
NON-GRASSES					
Amorpha canescens	2	3	3	44	45
Aster multiflorus	1	1	2	64	60
Callirrhoe alceoides	1	5	4	0	3
Erigeron ramosus	1	3	3	33	30
Hedeoma hispida	4	4	2	40	69
Lepidium virginicum	..	5	2	18	39
Plantago purshii	4	4	2	31	66
Rosa arkansana	4	4	4	13	18

the influence of late summer rains, caused the two sides of the prairie to differ so distinctly in appearance that a sharp line of demarkation was visible between them one year later, that is July, 1936 (Fig. 18). On the east side

FIG. 18. Carleton prairie, July, 1936. The central line of demarkation resulted from difference in dates of mowing the previous year.

of this line *Sporobolus asper, Bouteloua gracilis, B. curtipendula, Andropogon furcatus,* and Amorpha had flowered after mowing. Species on that side seemed also to have gained in vigor for *Andropogon furcatus, Amorpha,* and *Bouteloua curtipendula* were denser, greener, and taller than just over the line marking the different dates of mowing. On the west side *Bromus tectorum, Festuca octoflora,* and *Agropyron smithii* were better developed.

Permanent plots were established on 14 carefully selected areas and found to contain 49 species. They were widely spaced and included all the important grasses. The prairie was not mowed in 1936. Wheat grass had

FIG. 19. Tension lines at Carleton, August, 1937. Big bluestem (dark) held its ground against the newly established wheat grass (white) in favored areas.

extended its territory considerably in 1937, side-oats grama was more abundant, and all native grasses appeared in better condition than in 1936. In many local, well-defined areas big bluestem still held complete dominance, having repelled the invading wheat grass and most of the annual grasses so conspicuous over the prairie (Fig. 19). The line caused by the difference in mowing dates was obliterated by the tall wheat grass. A summary of the data on the 20 principal species in the quadrats is presented in Table 15.

TABLE 15. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT CARLETON, NEBRASKA

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	1,775	2,705	+ 52.4	14	0	0
Andropogon furcatus	925	645	— 30.3	12	0	0
Andropogon scoparius	1,134	172	— 84.8	8	1	1
Bouteloua curtipendula	1,244	1,322	+ 6.3	12	1	2
Bouteloua gracilis	779	405	— 48.0	9	1	4
Bromus tectorum	40	242	+505.0	8	3	1
Buchloe dactyloides	25.42*	2.79*	— 88.9	6	2	1
Carex	657	409	— 37.7	10	0	1
Festuca octoflora	(485)†	(830)†	+ 71.1	14	2	0
Koeleria cristata	434	29	— 93.3	10	0	5
Poa pratensis	384	708**	+ 84.4	11	0	3
Sporobolus asper	243	236	— 2.9	6	1	0
Stipa spartea	70	51	— 27.1	2	1	0
NON-GRASSES						
Amorpha canescens	52	31	— 40.4	7	0	0
Androsace occidentalis	41	405	+887.8	11	2	0
Aster multiflorus	879	392	— 55.4	10	1	2
Erigeron ramosus	75	110**	+ 46.7	9	6	0
Hedeoma hispida	104	697	+570.1	13	4	0
Lepidium virginicum	8	213	+2,562.5	13	9	0
Plantago purshii	42	367	+773.8	12	2	0

†Number of square decimeter units in which species occurred.
*Estimated cover in percent.
**Seedlings.

The deep-rooted Amorpha, occurring in 7 plots, suffered a loss of 40 percent. However, in the plots on the western side of the prairie the loss was 58 percent as compared with none on the eastern side which was mowed earlier. Aster was another deep-rooted species which decreased considerably. This is in accord with the long-known fact that because of the dryness of the subsoil below the claypan, alfalfa cannot survive drought on Crete silt loam. The loss for Aster was 68 percent on the west and 52 on the east side of the prairie. Other forbs with deep roots sustained smaller losses or none. Among the perennial grasses, buffalo grass, little bluestem, and June grass decreased by about 90 percent. Blue grama, big blustem, needle grass, and the sedges suffered smaller losses. Wheat grass made a large gain, side-oats grama a much smaller one. The large increase of bluegrass

was largely due to the appearance of a host of seedlings in one plot. Erigeron was present only as well developed seedlings, often 6 inches in height. Annual forbs as Androsace and Hedeoma and weeds such as Lepidium and downy brome gained more than 100 percent in these plots as well as becoming more widely distributed.

The percentage occurrence of the chief species in temporary random plots is given in Table 14 and may be considered as indicative of gain in territory occupied *(Festuca octoflora)*, of no change in distribution *(Bouteloua gracilis)*, or loss of territory *(Andropogon scoparius)*.

A clearer conception of the trends of change in floristic composition may be obtained by an examination of Table 16. Annual grasses, present in all permanent plots, had 5 times as many stems in 1937 as in 1936, but perennial grasses were 43 percent fewer. Among the forbs the story is similar, again reflecting the presence of the claypan. The short-lived, shallowly rooted weeds gained about 850 percent.

TABLE 16. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT CARLETON, NEBRASKA

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	21	13,125	7,741	— 41.0	14
Annual	2	53	274	+416.9	8
	1	(519)*	(830)*	+ 59.9	14
Perennial	18	13,072	7,467	— 42.9	14
Forbs	22	1,445	2,364	+ 63.5	14
Annual	8	352	1,665	+373.0	14
	1	(34)*	(65)*	+ 91.2	2
Perennial	13	1,093	699	— 36.0	12
Ruderals	6	48	457	+852.1	13
Total	49	14,579	10,528	— 27.8	14

*Number of square decimeter units in which species occurred.

The average number of species of grasses per plot decreased from 9 to 8, annuals gaining and perennials losing approximately 20 percent. Perennial forbs lost about 7 percent but annuals and weedy species increased sufficiently to raise the average total number of species from 14 to 15.6.

In the total area of 10 square meters quadrated, 14 of the square decimeter units were bare in 1936 but only 3 in 1937. The most active invaders of these bare areas were, in order of diminishing importance, Agropyron, Festuca, *Bouteloua curtipendula*, Androsace, and Hedeoma.

The vegetation averaged two thirds taller in 1937 than its level of 6 inches in 1936. Annual grasses were 120 percent taller but annual forbs only one third higher.

Tests of the rate of infiltration of water into soils supporting 3 species of grass in pure stands showed that for the first 2 inches applied there was little

difference in time required (Fig. 20). The rate for blue grama and western wheat grass was almost the same until the addition of the third inch. In the cylinder having the slowest rate of absorption in wheat grass, only half of the third inch was absorbed after 14.3 hours and water had penetrated only 8.5 inches. In another cylinder, the upper inch of claypan was found to be wet after 14 hours of watering in the swale having only 8 inches of porous topsoil.

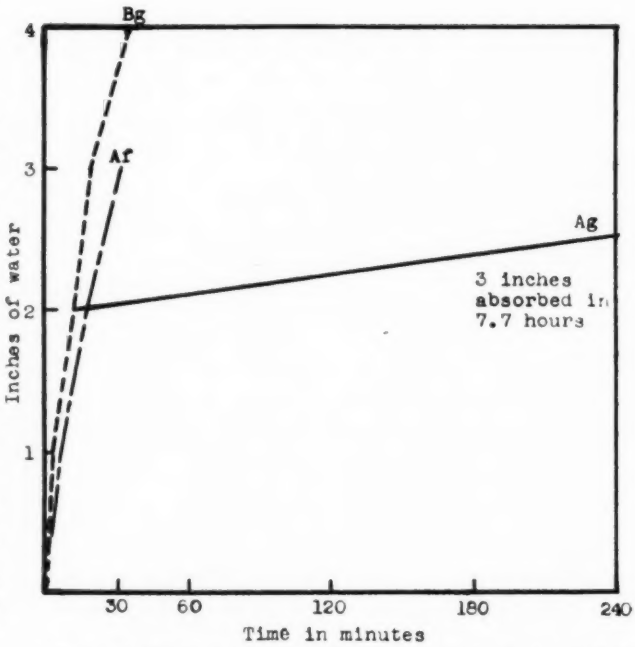

FIG. 20. Rate of infiltration of water into the soil in 3 types of vegetation at Carleton, Nebraska; blue grama (Bg), big bluestem (Af), and wheat grass (Ag).

A study of data given in Table 17 shows that in the wheat-grass swale the soil moisture was not depleted to such an extent as in well-drained soil occupied by big bluestem.

No moisture above the hygroscopic coefficient remained to a depth of 4 feet in the bluestem in August of both years. In the wheat grass it was exhausted in the upper 3 feet in 1936, but was present in small amounts at

TABLE 17. PERCENTAGE OF AVAILABLE SOIL MOISTURE IN TWO TYPES OF VEGETATION NEAR CARLETON, NEBRASKA

Depth in feet	Well-Drained Big Bluestem				Wheat-Grass Swale			
	Hygroscopic coefficient	1936	1937		Hygroscopic coefficient	1936	1937	
		Aug. 3	June 8	Aug. 11		Aug. 3	June 8	Aug. 11
0-.5	9.3	—3.3	20.0	—0.8	10.5	—3.7	12.0	1.8
.5-1	13.3	—1.6	7.3	—1.1	14.6	—0.3	—3.3	2.7
1-2	15.7	—0.9	8.0	—0.9	15.4	—0.3	3.9	1.6
2-3	12.9	0.0	2.7	—0.5	13.2	0.0	3.8	1.8
3-4	11.8	0.0	0.2	—0.3	11.6	0.7	2.2	2.8
4-5	12.0	0.9	...	0.3	11.9	1.2	...	3.8
5-6	12.4	1.0	...	0.4	12.2	2.6	...	4.2
6-7	12.0	2.0	...	1.0	12.2	2.9	...	7.6
7-8	11.6	4.0	...	1.9	11.4	5.7	...	7.4
8-9	11.0	4.3	...	...	11.9	5.8	...	...
9-10	11.2	4.7	...	...	11.6	6.4	...	...
10-11	10.9	5.8	...	...	10.9	8.3	...	...
11-12	9.9	6.6	...	...	8.3	7.9	...	...
12-13	9.5	6.4	...	...	10.3	6.2	...	...
13-14	9.7	5.3	...	...	13.2	6.4	...	...
14-15	10.7	5.3	...	...	14.0	5.9	...	...

most depths in 1937. Moisture content was less than the wilting coefficient of Briggs and Shantz (1912) to depths of 10 and 7 feet in big bluestem and in the wheat-grass swale, respectively, and at 10 to 15 feet the ratios were 1.02 to 1.1. Deep-rooted forbs were absent in the swale. At greater depths water was more plentiful during 1937 in the swale but less so in higher land. The higher hygroscopic coefficients at depths of 12 to 24 inches are correlated with the presence of the claypan, slow infiltration rate, rather dry subsoil, and high mortality among deep-rooted forbs.

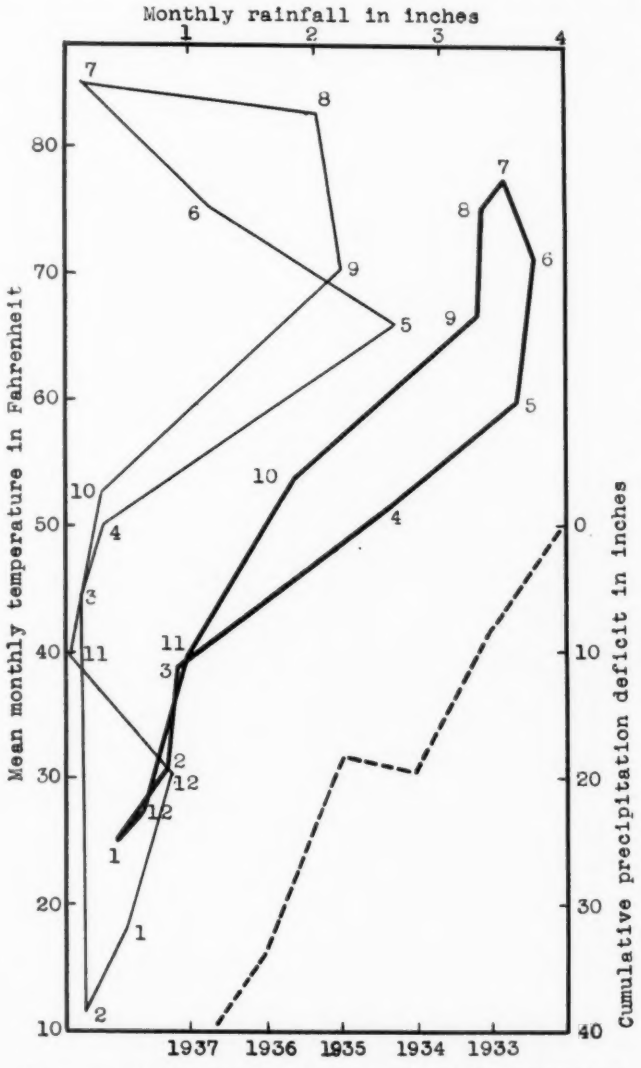

FIG. 21. Hythergraph of mean monthly temperature and rainfall for 1936 (light line) and for a 35-year period (heavy line) at Clay Center, Nebraska. The numbers 1 to 12 represent months. Broken line shows cumulative precipitation deficit from January, 1933, to August, 1937.

CLAY CENTER PRAIRIE

A well-drained, unbroken tract of about 10 acres lies 6 miles north of Clay Center, Nebraska. A shallow swale and an abandoned road cross it. As a rule the only disturbance has been annual mowing, but following the growing season of 1935 it was partially burned; in 1936 the vegetation was left intact. The soil is Hastings silt loam. It is readily penetrable by water and roots and has the lime layer at a depth of over 4 feet. This type of soil is considered excellent for corn and is almost entirely under cultivation in Clay County.

Prior to the drought, the dominant vegetation was a mixture of little bluestem of the bunch type and big bluestem. The former composed as much as 95 percent, and the latter frequently 20 percent of the vegetation. June grass, buffalo grass, and blue grama were fairly abundant while sand drop-

seed *(Sporobolus cryptandrus)*, six-weeks fescue, and wheat grass were present in small amounts. Lead plant was the most conspicuous forb.

The extent of drought injury to this prairie in 1934 and the damage by drought and dust in 1935 have been described by Weaver and Albertson (1936).

Clay Center received a total rainfall of 10.3 inches (40 percent of normal) in 1936. This was 3 inches less than in 1934, the driest previous year (Fig. 21). The mean summer temperature, which was 8.2° F. above normal in 1934, was 6.37° F. above the mean during 1936. The maximum temperature, 113° F., was the same each year. Two drought periods occurred in 1936. The first, of 24 days duration, began June 5 and was broken by a rain of 0.56 inch. It was immediately followed by a second of 37 days with only two measurable showers totaling 0.19 inch.

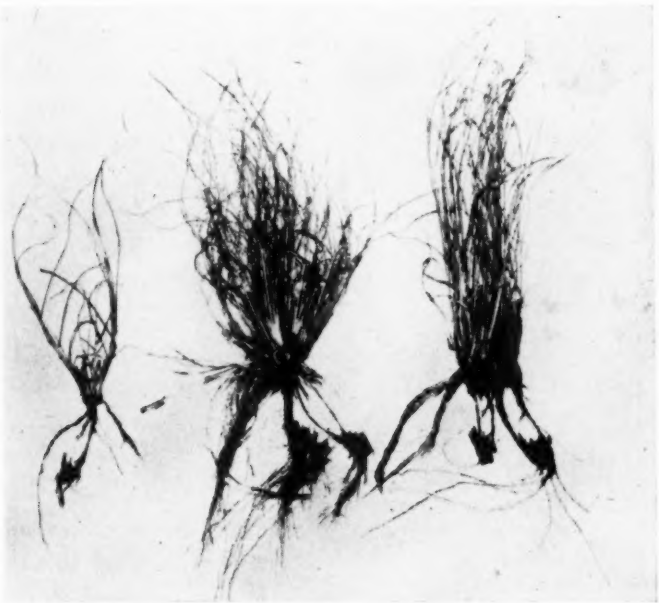

FIG. 22. Year-old bunches of *Bouteloua gracilis* attached by vertical rhizomes to the parent crowns which had been covered by 2 inches of dust in the early spring of 1935. Roots of the new crowns have been removed.

So weedy was this area in early July that only the presence of such deep-rooted forbs as Amorpha, Liatris, and Solidago proclaimed to the casual observer that it was unbroken prairie. Agropyron was the most abundant grass. It formed nearly pure stands on the higher ground where the dust deposited the previous year was 1 to 2 inches deep. The only other perennial grass to survive this burial was blue grama, which was able to develop rhizomes vertically and form new crowns on the surface (Fig. 22). Big bluestem was abundant but little bluestem and buffalo grass were scarce,

being outranked by June grass, side-oats grama, blue grama, Kentucky bluegrass, and sedges. The small panic grasses, especially *Panicum wilcoxianum,* were scattered everywhere. Many weedy types were scattered throughout. *Bromus tectorum* formed dense patches on lower ground, as did Plantago up the slope. Dense mats of seedlings of foxtail (*Setaria* spp.), red-root *(Amaranthus retroflexus),* and barnyard-grass *(Echinochloa crusgalli),* 2 to 3 inches tall and almost entirely dead, made up one third to one half of the cover. Abundance of other forbs was as follows in 1936 and 1937, respectively: Achillea, 5-0; Amorpha, 3-3; Aster, 1-3; Callirrhoe, 3-3; Hedeoma, 5-3; skeleton weed *(Lygodesmia juncea),* 3-4; *Meriolix serrulata,* 4-4; *Solidago glaberrima,* 1-3; and *S. mollis,* 3-3.

Eleven widely separated permanent meter quadrats were selected, one in each of several vegetation types. They included 51 of the 66 species observed here. A census was taken in the quadrats during the second week in July of each year. Table 18 shows that in these plots the perennial grasses reacted to the extreme conditions of 1936 and early 1937 in a strictly individual manner. The bouteloua, *Sporobolus asper,* and *Andropogon furcatus* held their own fairly well while the stems of *A. scoparius* were 65 percent fewer at the second counting. Losses of June grass, interstitial panic grasses, and Kentucky bluegrass were more than 80 percent, but this was partly offset

TABLE 18. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT CLAY CENTER, NEBRASKA

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	1,448	1,663	+ 14.8	6	0	0
Andropogon furcatus	525	506	— 3.6	10	0	1
Andropogon scoparius	494	173	— 64.9	4	0	0
Bouteloua curtipendula	340	344	+ 1.2	10	0	0
Bouteloua gracilis	2.12*	2.11*	— 0.5	7	0	1
Carex	588	675	+ 14.8	9	0	2
Koeleria cristata	282	32	— 88.7	6	0	3
Panicum scribnerianum	226	44	— 80.5	5	0	2
Panicum wilcoxianum	514	37	— 92.8	8	0	3
Poa pratensis	498	95	— 80.9	9	0	5
Schedonnardus paniculatus	107	406	+279.4	2	0	1
Sporobolus asper	45	45	0	3	2	0
Sporobolus cryptandrus	113	142	+ 25.7	7	0	4
NON-GRASSES						
Amorpha canescens	26	14	— 46.1	5	0	1
Artemisia gnaphalodes	315	448	+ 42.2	8	0	2
Aster multiflorus	237	262	+ 10.5	5	1	0
Callirrhoe alceoides	52	74	+ 42.3	5	1	2
Lepidium virginicum	8	155	+1,837.5	10	8	0
Salsola pestifer	4	221	+5,425.0	11	8	0
Solidago glaberrima	434	307	— 29.3	7	0	1

*Estimated cover in percent.

by gains of Texas crabgrass *(Schedonnardus paniculatus)*, sand dropseed, wheat grass and sedges.

Perennial grasses as a group decreased in density 15 percent while annual grasses increased 10 percent (Table 19).

TABLE 19. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT CLAY CENTER, NEBRASKA

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	21	7,200	6,220	—13.6	11
Annual	7	443	487	+ 9.9	7
Perennial	14	6,757	5,733	—15.2	11
Forbs	20	1,196	1,178	— 1.5	11
Annual	5	13	17	+30.8	8
Perennial	15	1,183	1,161	— 1.9	11
Ruderals	15	561	937	+67.0	11
Total	54	8,518	7,852	— 7.8	11

It may be seen in Table 18 that five of the species which dropped out of a greater number of plots than they invaded were species that made definite gains in abundance. The data show that there was a strong tendency among these species for larger plants and denser stands to increase while small plants and sparse stands died. That the development of above-ground parts of a species is proportional to that of roots is well known, and considerable data indicate that deep roots and drought resistance are closely related in prairie plants.

Perennial forbs were also inconsistent, Artemisia gaining 42 percent and Missouri goldenrod losing 29 percent. For the group, gains nearly made up the losses. Annual forbs increased one third and weeds two thirds with percentage increases of Salsola and Lepidium in the thousands. In several plots in 1936, the hundreds of dry weed seedlings less than 3 inches tall were not counted but their percentage cover merely noted. In 1937 these areas were bare but overshadowed by fewer, larger plants of Salsola and other weeds (Fig. 23).

The unusually large number of species per quadrat (14.4) in 1936 was only one less the following year. Annual and perennial grasses and perennial forbs decreased while weeds and annual forbs increased in number of species per plot.

Of the 1,100 square decimeter units in the quadrats, 59 were bare in 1936 and 136 in 1937. However, only 16 were bare both years. The large scale depopulation accompanied the disappearance of 26 species from the unit areas. Chief among these were the weeds, red-root, stink-grass *(Eragrostis major)*, and foxtail, the grasses, Poa, *Panicum wilcoxianum*, and Koeleria, and the

forb, *Solidago glaberrima*. Salsola, *Bromus tectorum*, Artemisia, Lepidium, and Agropyron were the foremost of the 19 species of invaders.

Certain changes, though not shown by the plots, were obvious. The lush vegetation of June, having used the surface moisture, was very dry on July 10 (Table 20). The early annual weeds, unusually large because of reduced competition, were no longer making demands on the habitat, but were breaking the force of the hot winds and casting slight shade over the withering grasses. Wheat grass had spread over most of the area, and the large, well-developed bunches of the grama grasses were quite conspicuous. Downy brome appeared to dominate the lower side of the prairie.

FIG. 23. Clay Center prairie in July, 1937. *Artemisia gnaphalodes* (white) with a height of 14 inches was overtopped only by wheat grass. It was the most conspicuous plant on the prairie.

Rates of infiltration in 4 types of vegetation were compared on August 17. Soil moisture had been slightly replenished since July 10 by eight showers totaling 3.8 inches (Table 20).

TABLE 20. PERCENTAGE OF AVAILABLE SOIL MOISTURE DURING THE SUMMER OF 1937 AT CLAY CENTER, NEBRASKA

Depth in feet	Hygroscopic coefficient	June 7	July 10	August 17
0-1	8.4	18.1	-0.9	2.5
1-2	9.5	5.4	0.0	1.2
2-3	10.5	1.7	0.9	1.2

In the lead plant, side-oats grama, and blue grama types, the 4 inches of water penetrated very rapidly and with no marked difference in rate according to type. Neither was there any relation between the number of stems

enclosed by a cylinder and the rate of infiltration. Among the three types, the greatest variation between the fastest and slowest rate per cylinder was from 10 to 24.5 minutes, the average time being 14.7. The four cylinders, pressed into the ground through two inches of dust, which had not been disturbed since its deposition in March, 1935, required an average time of 28 minutes for 4 inches of water to penetrate, and ranged from 21 to 35 minutes (Fig. 24). Thus, soil bearing either grasses or forbs absorbed twice as rapidly as bare, consolidated dust.

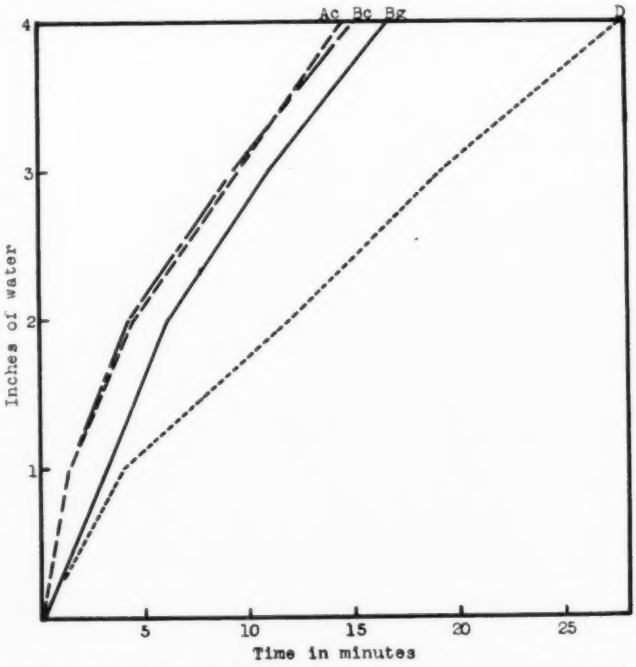

FIG. 24. Rate of infiltration of water into the soil in 4 types of vegetation at Clay Center, Nebraska; lead plant (Ac), side-oats grama (Bc), blue grama (Bg), and a deposit of dust 2 inches deep (D).

The composite of random soil samples taken to a depth of 2 inches and kept watered in the greenhouse for 5 months yielded more than 300 plants of 21 species. Perennials constituted 29 percent of the species but only 3 percent of the seedlings. Six-weeks fescue was the most abundant species, with downy brome next in rank.

NELSON PRAIRIE

This is an upland prairie of 20 acres 5.5 miles northeast of Nelson, Nebraska. It slopes gently eastward to drop abruptly near its edge into ravines which together include not more than one tenth of the area.

The soil of the upland is Crete silt loam, as at Carleton.

In 1931, the dominant vegetation was *Andropogon scoparius* with a good mixture of *A. furcatus*. Alternes of *Bouteloua gracilis* occurred and in them there was an abundance of Plantago, Hedeoma, and Festuca. *Bromus tectorum* was an invader. Although the prairie was very grassy, both grasses and forbs were of small stature and the latter were less abundant than farther eastward.

In 1935 only remnants of little bluestem were found, and big bluestem was greatly depleted by drought and wind-deposited soil. Side-oats grama and blue grama also were injured, while wheat grass had invaded. Festuca

occurred in as many as 212 bunches per square meter on the upper, dust-covered half of the slope where it was codominant with downy brome. Where this deposit approached an inch in depth, small, thriving alternes of wheat grass were present. The usual interstitial plants were rare and more than two thirds of the ground was bare.

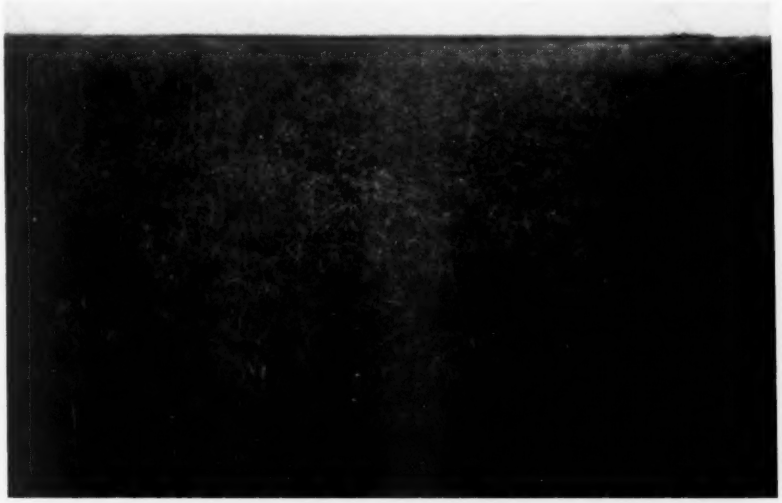

FIG. 25. Big bluestem buried by silt in 1936 at the Nelson prairie.

The vegetation of this prairie, when examined on July 4, 1936, appeared to be in a critical condition. Two days previously a local cloudburst accompanied by much hail and violent wind had laid the already dwarfed vegetation still lower and covered much of the grass with eroded topsoil and debris. The absence of leaves on all but the protected south sides of plants, and the bruised stems of such forbs as Liatris, Kuhnia, and Amorpha bore witness of the direction and severity of the storm. Such mature and brittle plants as Festuca and Erigeron were pelted into the ground, which was packed very hard, or washed down the slope to lodge in small dams against living clumps or stems. Numerous, widely branching cracks were everywhere on the upland, where they must have received considerable runoff from intervening areas as well as from the field above the prairie. In a swale at the north end, some of the best big bluestem on the prairie was buried under 4 to 6 inches of alluvium (Figs. 25 and 26).

In early August the vegetation was drought stricken. The cumulative rainfall deficiency had nearly doubled since 1934. The average mean temperature for the 3 summer months was 6.7° F. above normal, 2.2 degrees less than for 1934 (Fig. 27).

Nevertheless, an impressive change of aspect had been wrought in the vegetation since July 4. Viewed from the sky the prairie would have appeared as a network of green spread over a gray-brown field. The soil cracks had

not closed but presented a border of 8 to 12 inches on each side consisting of a lush growth of big and little bluestems and side-oats grama. Leaves and racemes of the last were 8 and 20 inches tall, respectively. Away from the cracks, much big bluestem had made no growth during July while the rest had grown slightly at the base. Little bluestem, however, had put out many new stems and was much more conspicuous than a month earlier. No efficient rain had fallen since the cloudburst, and no moisture above the hygroscopic coefficient was present, except near the cracks, at least to a depth of 3 feet (Table 22).

FIG. 26. The same area dominated by downy brome in 1937.

Big bluestem and six-weeks fescue were the most abundant grasses, with little bluestem and side-oats grama next in rank. Wheat grass was common, but only one percent had spikes. Only one clump of hairy grama *(Bouteloua hirsuta)* was found. Sand dropseed was more abundant on a ridge in the center of the prairie than elsewhere. Here it was mixed with wheat grass, plantain, peppergrass, and blue grama, the total basal cover scarcely exceed-

TABLE 21. RELATIVE IMPORTANCE OF THE CHIEF FORBS AT NELSON, NEBRASKA, EXPRESSED IN ABUNDANCE CLASSES. CLASS VALUES AS IN TABLE 7

Species	1931	1936	1937
Amorpha canescens	3	3	3
Antennaria campestris	1	0	0
Aster multiflorus	1	3	4
Erigeron ramosus	3	3	4
Hedeoma hispida	3	4	3
Kuhnia glutinosa	3	4	4
Lepachys columnaris	2	4	0
Lepidium virginicum	0	3	2
Liatris punctata	1	3	4
Plantago purshii	3	2	3
Solidago glaberrima	3	5	0

ing one percent. During the first night on the prairie .5 inch of rain fell slowly and by morning near the cracks the inflorescences of big bluestem, which were not visible in the evening, had unfolded at a height of 28 inches.

Relative abundance of the important forbs is shown in Table 21. It was obvious that deep-rooted perennials had not been able to maintain their former density after the drought of 1936.

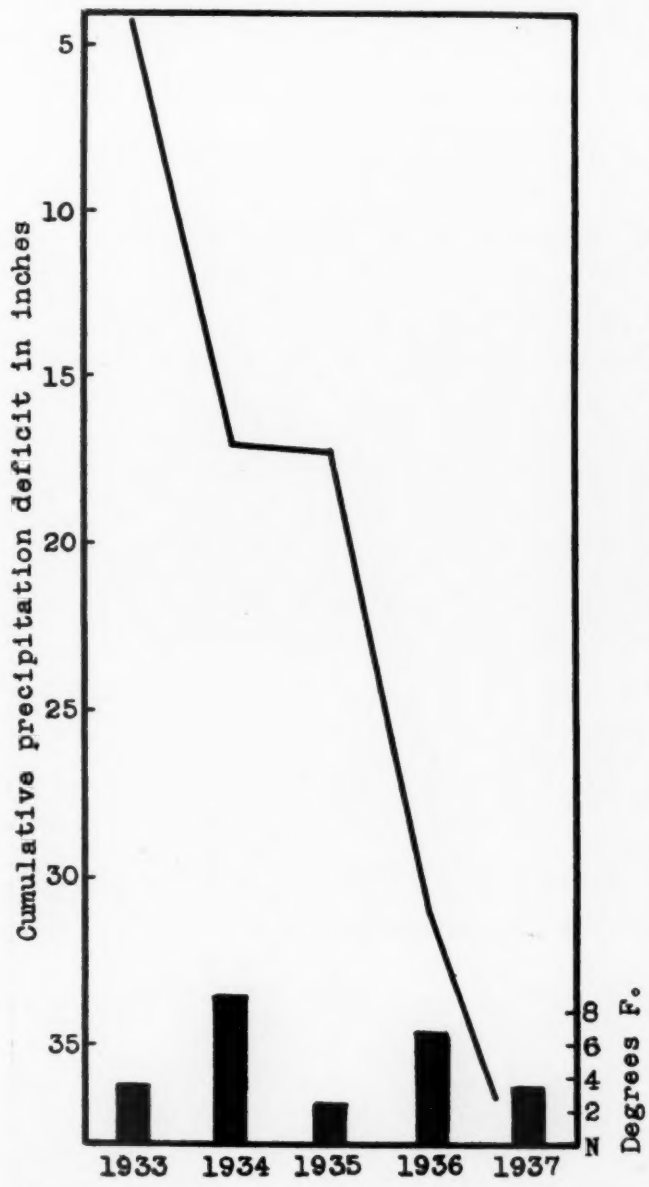

FIG. 27. Cumulative precipitation deficit from January 1, 1933 to August 31, 1937 (line) and average mean monthly departure above normal temperature for June, July, and August (bars) at Nelson, Nebraska. Temperature data are based on records from three nearest Weather Bureau stations.

Selection of 8 permanent plots with a total area of 16 square meters was made in 6 different types of vegetation on the upland, and a census was taken during the second week of August each year.

In early June, 1937, the higher one fourth of the prairie was found to be buried under eroded topsoil from the field above to a depth of 2 inches. Only the stiffer forbs, wheat grass and a scattering of big bluestem were able to emerge through this deposit. It was largely populated by the annual foxtail, pigweeds, Russian thistle, and downy brome. The cracks, though still open, seemed to be of small benefit to the vegetation, as it was equally dwarfed everywhere. The cracks evidently permitted rapid evaporation as well as rapid entry of water. The topsoil was moist but the second foot was extremely dry (Table 22).

Precipitation for all but three months since the previous visit had been below normal and the winter had been especially dry and cold. The approximately normal precipitation of 6.3 inches during June and July, however, was sufficient to increase soil moisture slightly below the first foot, and to improve the condition of the vegetation somewhat. By the middle of August the grasses along the cracks were again flourishing although dwarfed elsewhere. This formed a pattern visible a quarter of a mile away (Fig. 28).

TABLE 22. PERCENTAGE OF AVAILABLE SOIL MOISTURE ON THE UPLAND AT NELSON, NEBRASKA

Depth in feet	Hygroscopic coefficient	August 6 1936	June 7 1937	August 16 1937
0-1	9.8	-1.7	5.3	1.3
1-2	12.4	-0.6	0.6	2.8
2-3	12.1	-0.7	0.7	2.0

Side-oats grama and sand dropseed were abundant and conspicuous among the generally distributed but dead Festuca, Bromus, and Plantago. Wheat grass was not fruiting. Indeed its presence was revealed only by careful search. Many of its stiff, dry spears 4 to 5 inches tall were dead and decayed at the soil surface. Several new clumps of hairy grama were found and the one old clump previously noticed had 42 percent more stems. The character of the cover on the lower half of the prairie is well represented in Figure 29. The plot census data confirmed, in the main, the general observations (Table 23).

FIG. 28. Lush growth of grass along cracks at Nelson, Nebraska, August, 1937.

Although already decimated by the drought of 1934, big and little bluestems, in 6 and 4 plots, respectively, were again reduced. The same was true of June grass, bluegrass, and the small panic grasses, but the losses were still greater. Wheat grass, usually on the increase, had all but disappeared while the three grama grasses showed gains ranging from 26 to 87 percent. Sand dropseed was 3 times as abundant. Among the deep-rooted perennials only Amorpha held its own while Kuhnia and Liatris were much less numerous in the permanent plots in 1937. Artemisia and Aster had disappeared.

FIG. 29. Open cover typical of the lower half of the Nelson prairie in 1937.

Of the five groups compared in Table 24, four lost and one (annual grasses) made only a slight gain. The loss of perennial grasses, although smaller in percentage than that of forbs, signifies a much greater lowering of the total density.

Annuals of all kinds appeared to be as generally distributed in 1937 as in the preceding year. The number of species of weeds per plot was larger the second year, but perennial forbs lost nearly one and perennial grasses more than two species per plot. The average total number of species per plot, however, remained nearly constant (Table 24).

The number of bare square decimeter units had increased 56 percent.

TABLE 23. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT NELSON, NEBRASKA

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	550	108	— 80.4	3	0	0
Andropogon furcatus	700	409	— 41.6	6	0	1
Andropogon scoparius	568	147	— 74.1	4	0	1
Bouteloua curtipendula	1,133	2,123	+ 87.4	6	0	0
Bouteloua gracilis	459	579	+ 26.1	2	0	0
Bromus tectorum	116	47	— 59.5	3	0	1
Carex	195	187	— 4.1	6	0	2
Festuca octoflora	(309)*	(410)*	+ 32.7	6	0	0
Koeleria cristata	227	13	— 94.3	5	1	3
Panicum scribnerianum and *P. wilcoxianum*	24	3	— 87.5	3	0	2
Poa pratensis	136	0	—100.0	5	0	5
Schedonnardus paniculatus	128	65	— 49.2	2	0	1
Sporobolus cryptandrus	25	83	+232.0	4	1	0
NON-GRASSES						
Amorpha canescens	187	184	— 1.6	2	0	0
Aster multiflorus	36	0	—100.0	2	0	2
Erigeron ramosus	106	1	— 99.1	3	0	2
Plantago purshii	(133)*	(113)*	— 15.0	4	0	0
Salsola pestifer	0	23	+	3	3	0

*Number of square decimeter units in which species occurred.

TABLE 24. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT NELSON, NEBRASKA

	Number of species	Number of Stems		Percentage of change	Number of plots	Species Per Plot	
		1936	1937			Average 1936	Percentage of change 1937
Grasses	18	4,233	3,793	—10.4	7	9.2	— 25.4
Annual	4	(427)*	(457)*	+ 7.0	6	1.5	+ 10.7
Perennial	14	4,233	3,793	— 10.4	7	7.7	— 32.6
Forbs	11	388	244	—37.1	7	2.8	—23.3
Annual	3	133	59	—55.6	6		
	1	(133)*	(113)*	—15.0	4	1.7	+ 9.6
Perennial	7	255	185	—27.5	5	1.2	—71.8
Ruderals	5	(118)*	(47)*	—60.2	6	.67	+173.1
Total	33	4,622	4,061	—12.1	8	10.5	— 1.9

*Number of square decimeter units in which species occurred.

This depletion in cover was caused largely by the death of Festuca, Erigeron, *Bouteloua curtipendula,* and *Andropogon furcatus.* Festuca, *B. curtipendula,* and Hedeoma were the chief invaders of the units bare in 1936.

The infiltration rate of water into soil bearing three types of vegetation was measured (Fig. 30). The cylinders were placed so as to enclose bunches

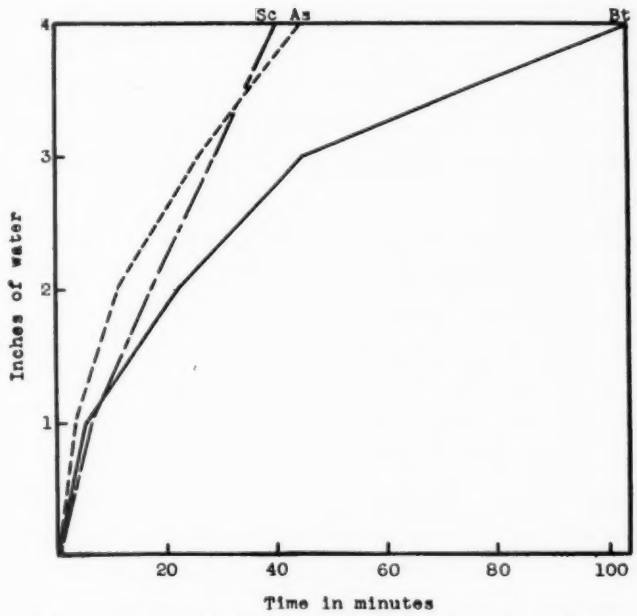

FIG. 30. Rate of infiltration of water into the soil in 3 types of vegetation at Nelson, Nebraska; sand dropseed (Sc), little bluestem (As), and downy brome (Bt) on an alluvial deposit one year old.

of sand dropseed and of little bluestem a few feet distant; also in the alluvium covered by downy brome which is shown in Figure 29. Soil in the little bluestem type absorbed the first 2 inches more rapidly and the last 2 more slowly than did the sand dropseed type. It required 44 minutes as compared with 40 minutes in the latter for the absorption of 4 inches of water. In the alluvium average time for 4 inches was 104 minutes. The first inch of water disappeared in 5.7 minutes but the rate gradually lessened, the fourth inch requiring 59 minutes. In no instance was there any correlation between the amount of visible vegetation enclosed by the cylinders and the rate of infiltration.

MONTROSE PRAIRIE

Four miles southeast of Montrose, Kansas, there is a rectangular upland prairie of about 20 acres undisturbed except by frequent burning. On the east it is bordered by a newly-fenced 30-acre pasture which in 1931 was part of this ungrazed prairie. Other contacts are with cultivated fields. The relatively level north end is separated from the long, north-sloping southern part by a shallow ravine which drains across it eastward from the plowed field. The soil in the ravine is Lincoln silt loam, colluvial phase; that of the slopes is Colby silty clay loam, which comprises 95 percent of the prairie. The 6-inch layer of eroded topsoil is a dark, pervious mantle of silt loam underlain by a subsoil consisting of about 20 inches of grayish to light brown, slightly compacted silty clay loam above unweathered loess. Bennett (1935) reports that on this soil type little bluestem and grama grass were over 3,000 times as effective as clean cultivated Kafir corn in preventing erosion, and 400 times in preventing runoff.

In 1931 most of the area was dominated by a mixture of *Andropogon furcatus* and *A. scoparius,* the former (mixed with *Sorghastrum nutans*) having full possession of protected slopes and ravine bottom while the latter

increased to 80 percent of the mixture on much of the higher ground. *A. scoparius* was present in both the sod and bunch types. *Bouteloua curtipendula* and Koeleria were common, especially on dry slopes. A few spears of Agropyron, as well as tufts of Buchloe and *Bouteloua gracilis,* were present but nowhere abundant. *Sporobolus cryptandrus* and *S. asper* were uncommon.

Study of the area in July, 1936, revealed a vegetation characterized by a singular uniformity in height and composition. Alternes were relatively few, being restricted to 2 or 3 of Agropyron and *Andropogon furcatus,* unless several patches of *Bouteloua gracilis* and *B. curtipendula* only 1 to 5 square feet in area are included. Big bluestem was in unusually good condition immediately surrounding numerous small piles of hay—old haycocks and accidental leavings. It was still abundant over the prairie as a whole but was at least equaled in abundance by Agropyron. *Bouteloua curtipendula* and *B. gracilis* were almost as important as *Andropogon furcatus. A. scoparius,* Buchloe, Poa, Elymus, and *Panicum virgatum* were not common; *P. scribnerianum,* Sorghastrum and Schedonnardus were rare; but *Sporobolus cryptandrus* and *S. heterolepis* were not seen.

Artemisia, Allionia, Kuhnia, Rosa, Linum, Sideranthus, Vernonia, Aceratates, and Lepachys appeared to be as abundant as described by Weaver before the drought. Amorpha (the only conspicuous forb), Aster, Solidago, Psoralea, and Antennaria, though still present, had decreased in abundance while Astragalus, Silene, Physalis, Salvia, and Liatris could no longer be found. On the other hand, Hedeoma had increased so that much of the ground fairly bristled with it. Androsace, Chenopodium, Ambrosia, Tithymalus, Lepidium, Salsola, and *Eragrostis major* were present although not recorded here before the drought. Where possible, members of the above groups are listed in order of decreasing abundance in 1936. The increase in ruderals, although primarily due to drought disturbance, was greatly abetted by the presence of numerous weedy stack sites and by the extreme weediness of adjacent fields.

One of the chief ecological features of this prairie was an area near the top of the hill at the south end which, in the spring of 1935, had been buried under a deposit of wind-blown gray dust ranging in depth from one foot near the fence to one-fourth inch six rods down the slope. The dust came from the adjacent field and had been deposited in this short distance after entering the prairie. A rather pure stand of wheat grass with a scattering of big bluestem and weeds formed a very open cover, considerable areas being nearly bare and quite unprotected from sheet erosion except by the interlacing rhizomes of Agropyron in the surface soil. At the shallower edge of the deposit, many dead crowns and rhizomes of little bluestem, side-oats

grama, and big bluestem lay exposed on the surface and to 1.5 inches above it, suggesting that, after covering them, the dust plus some of the original topsoil had been eroded away by water in the absence of any living protective cover. Dust deeper than 0.5 inch appeared to have destroyed most of the big bluestem, and that deeper than 1 inch, all of it. Wheat grass was fruiting here and in a few other scattered spots.

About midway down the long north slope, a belt of fine big bluestem 1 to 2 rods wide extended across the prairie from the east as if acting as a barrier to the invading horde of Agropyron descending the slope. Below it, Agropyron occurred in only a few scattered patches and in the ravine bottom. In this alterne of big bluestem, smooth sumac *(Rhus glabra)*, a shrub common to forest-prairie ecotones, was present in considerable numbers in spite of annual mowing.

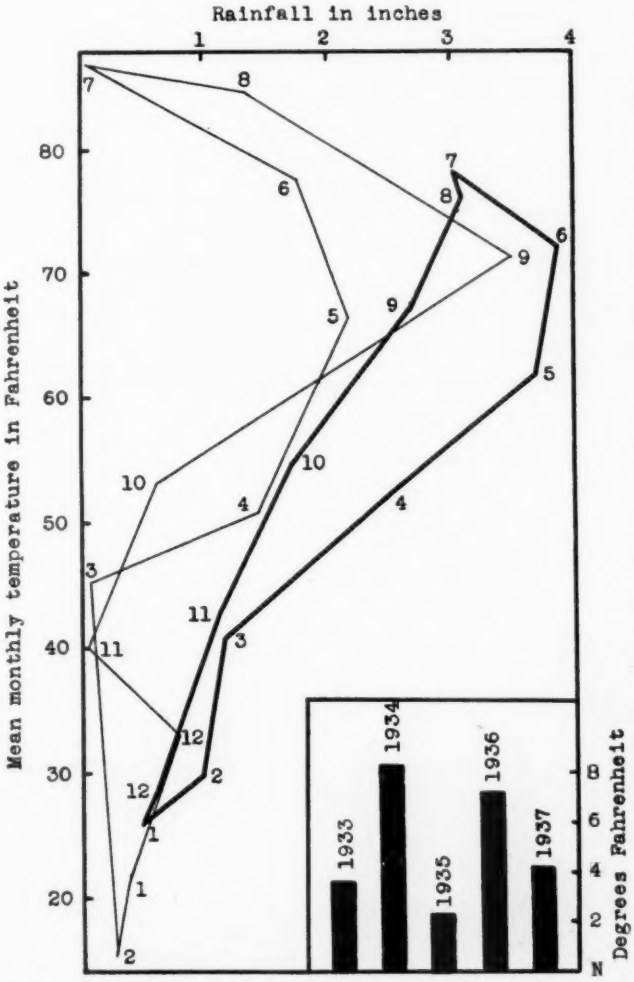

FIG. 31. Hythergraph of mean monthly temperature and rainfall for 1936 (light line) and for a 36-year period (heavy line) at the Montrose prairie. The numbers 1 to 12 represent months. Inset: Departure above the normal mean temperature for 3 summer months.

The condition of the vegetation was again noted a month later. During the interim 0.04 inch of rain had fallen and the mean temperature had been nearly 9° F. above normal (Fig. 31). On the upper slope wheat grass had produced heads on about one fourth of the plants and most of the leaf bases were green. Big bluestem was brittle to within an inch of the ground, having made no additional growth. The leaves of blue grama were dry 3 inches from the tip, but side-oats grama was still green though not in flower. Artemisia was drying up without flowering; Kuhnia was three-fourths defoliated and

half the leaves of *Solidago mollis* were dead, but *Allionia linearis* was flowering. Only the older plants of buffalo grass had any green leaves.

Twelve permanent plots with a total area of 10.5 square meters were located in eight different types of vegetation widely distributed over the area. These were quadrated about July 1 during both years. The most readily observed change was that produced by the great extension of wheat grass. It had migrated down the slope and across the ravine from its previous position on the dust deposit, which was now cemented so firmly that a steel quadrat pin could be forced into it only with difficulty. All grasses were in a condition of reduced activity and cracks in the soil were beginning to open. *Andropogon scoparius* and Poa appeared to have been reduced, but Buchloe seemed more abundant. A part of the data for 20 chief species included in the permanent plots is given in Table 25.

TABLE 25. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES, TOTAL NUMBER OF PLOTS OCCUPIED BOTH YEARS, AND NUMBER INVADED OR VACATED BY SPECIES IN 1937, AT MONTROSE, KANSAS

Species	Number of Stems		Percentage of change	Number of Plots		
	1936	1937		Total	Invaded	Vacated
GRASSES						
Agropyron smithii	1,588	2,688	+ 69.3	11	0	0
Andropogon furcatus	1,714	869	— 49.3	12	0	1
Andropogon scoparius	211	42	— 80.1	3	1	0
Bouteloua curtipendula	4,935	4,513	— 8.6	10	0	0
Bouteloua gracilis	0.96*	1.61*	+ 67.7	6	0	1
Buchloe dactyloides	47.57*	59.75*	+ 25.6	3	1	0
Carex	301	240	— 20.3	10	0	1
Festuca octoflora	28	1,446	+5,064.3	11	8	0
Koeleria cristata	65	34	— 47.7	2	0	1
Panicum scribnerianum	197	7	— 96.4	5	0	2
Panicum virgatum	30	0	—100.0	2	0	2
Poa pratensis	140	207	+ 47.8	1	0	0
NON-GRASSES						
Allionia nyctaginia	15	14	— 6.7	3	1	1
Amorpha canescens	70	43	— 38.6	6	0	1
Androsace occidentalis	21	345	+1,542.9	7	3	0
Aster multiflorus	133	68	— 48.9	8	0	1
Erigeron ramosus	36	58	+ 61.1	4	1	0
Hedeoma hispida	39	491	+1,159.0	10	4	0
Lepidium virginicum	4	122	+2,950.0	7	4	0

*Estimated cover in percent.

The native mid and tall grasses all appeared to have suffered losses ranging from 100 percent among the panic grasses to 9 percent for *Bouteloua curtipendula*. Increase in abundance was shown by wheat grass, blue grama, and buffalo grass, all species characteristic of mixed prairie. Little bluestem was an exception as it had only 20 percent as many stems in 1937 as in 1936. Festuca, an annual grass, Lepidium, an annual weed, and Hedeoma, an annual forb, all increased enormously while Aster and Amorpha, deep-rooted perennial forbs, suffered marked losses.

The 12 plots were found to contain 56 of the 72 species listed. The trends of change in floristic composition are summarized in Table 26.

Although the grasses originally producing the best hay decreased, perennial grasses as a group remained constant. Because of the larger number of annuals, forbs as a class increased although the number of perennials was greatly reduced.

TABLE 26. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS AT MONTROSE, KANSAS

	Number of species	Number of Stems		Percentage of change	Number of plots
		1936	1937		
Grasses	18	22,074	22,093	+ 0.1	12
Annual	3	(49)*	(254)*	+418.4	10
Perennial	15	22,074	22,093	+ 0.1	12
Forbs	24	377	1,068	+183.3	12
Annual	6	91	905	+894.5	11
Perennial	18	286	163	— 43.0	12
Ruderals	14	105	168	+ 60.0	10
Total	56	22,556	23,329	+ 3.3	12

*Number of square decimeter units in which species occurred.

At the second quadrating, the average number of species per plot had increased only 1.8 percent but changes shown by the different ecological groups were more marked. Gains ranged from 232 percent and 100 percent for species of annual grasses and forbs, respectively, to 25 percent for weeds. Perennial grasses had 18 percent and perennial forbs 37 percent fewer species per plot. In 1936 the numbers of species per plot were: total, 11; annual grasses, .25; perennial grasses, 6.3; annual forbs, 1.25; perennial forbs, 2.5; and weeds, 1.0. Certain annual grasses are weeds.

The vegetation was about 7 percent taller than the 1936 average of 11 inches. Grasses and forbs showed approximately the same increase in height.

Fifty of the 1,050 square decimeter units in the plots were without vegetation in 1936, and the following year 43 were bare, although only 11 were bare both years, *i.e.* 39 were invaded and 32 depopulated between studies. Agropyron was the chief invader (27 squares) followed by Festuca, Hedeoma, and *Bouteloua curtipendula*. A few bunches of the last exhibited a diseased condition characterized by dwarfing, chlorosis, and excessive proliferation. Agropyron, *Bouteloua curtipendula*, *Amaranthus* spp., and *Andropogon furcatus* were most important of those creating bare areas by their death.

Soil samples taken at 6 different places were found to be very uniform as to structure, color, compaction, and moisture content at corresponding depths, regardless of vegetation type. For example, samples taken at a depth of 12 to 24 inches on the upper slope in the big bluestem alterne, in wheat grass seven yards distant, and in Kentucky bluegrass near the bottom and at

the upper north side of the ravine contained 16.1, 16.3, 16.1 and 16.0 percents of water, respectively. To a depth of 4 feet on the upper slope and to three feet near the ravine, there was no soil moisture above the hygroscopic coefficient on August 5, 1936. This is understandable in the light of temperature and precipitation data shown in Figure 31. Every month of 1936, up to and including August, was drier than normal while the mean temperatures of the three summer months averaged 7.6° F. above normal. The 20.65 inches of moisture received during the next 11 months was 1.2 inches below normal and effected an increase in moisture content of only the upper 4 feet of soil, but this was largely exhausted in the second to fourth feet during the next six weeks. The available moisture in the surface foot was provided by a 0.6-inch rain 6 days before the samples were taken (Table 27).

TABLE 27. PERCENTAGE OF AVAILABLE SOIL MOISTURE AT CORRESPONDING PERIODS IN 1936 AND 1937 AT MONTROSE, KANSAS

Depth in feet	Upper Slope				Lower Slope			
	Hygroscopic coefficient	Aug. 5 1936	June 30 1937	Aug. 13 1937	Hygroscopic coefficient	Aug. 5 1936	June 30 1937	Aug. 13 1937
0-.5	9.2	—1.6	1.2	3.3	....	...	...	...
.5-1	12.3	—1.0	2.1	0.4	10.4	—1.7	—0.6	1.5
1-2	15.5	—0.6	4.0	—0.9	14.4	—1.1	2.3	—1.2
2-3	13.3	—0.6	2.8	—1.2	12.0	—0.3	3.5	1.0
3-4	13.0	—1.5	0.0	—0.5	11.5	1.0	1.0	1.4
4-5	12.0	0.2	...	1.0	10.4	3.0	...	4.2
5-6	11.1	1.6	...	2.8	11.9	5.5	...	3.3
6-7	10.8	2.6	...	...	12.1	3.5	...	...
7-8	12.3	2.8	...	...	12.4	5.8	...	...
8-9	13.3	3.5	...	...	13.0	6.2	...	...
9-10	14.3	4.9	...	...	14.0	6.8	...	...
10-11	14.6	6.2	...	...	13.9	7.9	...	...
11-12	14.9	6.1	...	...	14.6	7.0	...	...

Rates of infiltration of water into the soil in four types of vegetation were somewhat different. The first inch required periods ranging from 3.5 minutes in Amorpha to 9.5 minutes in Agropyron on the dust deposit 250 yards distant. The 4 cylinders were placed around 2, 3, 5, and 7 stems of Amorpha, a shrubby species having a long taproot. Time required for the 4 inches to enter the ground ranged from 28 minutes where 3 stems were enclosed to 68 minutes where 2 stems were present, and averaged 53 minutes for the replication of four. In Buchloe, five rods distant on the same level, the rate for each inch was approximately the same as for Amorpha, and the range among cylinders was 29 to 72 minutes (Fig. 32). Except for the first inch, the rate in the alterne of *Andropogon furcatus* previously described was considerably the highest of 4 types. The average time for 4 inches was 34.2 minutes, the range being from 20 to 52 minutes. Again no correlation could be shown to exist between the number of shoots included within the cylinder and the infiltration rate. In the wheat grass growing on a dust deposit, the

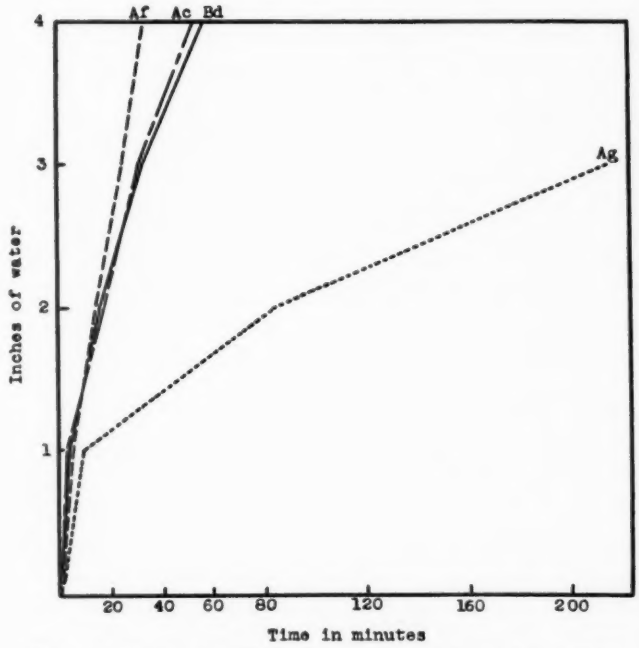

FIG. 32. Rate of infiltration of water into the soil in 4 types of vegetation at Montrose, Kansas; big bluestem (Af), lead plant (Ac), buffalo grass (Bd), and wheat grass (Ag).

average rates were 9.5, 75, and 132 minutes for inches 1 to 3, respectively. The range was from 39 to 474 minutes for three inches and in this instance the larger the number of plants per cylinder, the more rapidly the water was absorbed.

Seeds of 18 species were present in the composite of 20 random shallow soil samples taken from this prairie in August, 1937. Of the seedlings appearing during 5 months in the greenhouse, one seventh of the plants and one sixth of the species were perennials. Nearly half of the seedlings were ruderals, but the most abundant species was an annual grass, *Festuca octoflora.*

DISCUSSION

A study of the data from the 9 prairies reveals that native perennial grasses and forbs suffered a further reduction in density following the drought of 1936 (Table 28). At some time during each summer soil moisture was non-available to a depth of 4 feet. On the upland, less than 2 percent was available to 8 feet. The zone in which the activity of roots has but slight effect upon soil moisture content thus appears to lie below 8 feet in upland prairies of this region. Weaver (1920) used the bisect method on upland prarie to ascertain that few grasses penetrate deeper than 5 feet, and few forbs deeper than 8 feet. During the drought of 1934, Nedrow (1937) showed that Antennaria, *Poa pratensis* and *Panicum scribnerianum* did not recover from wilting when watered at a depth of 32 inches, while *Andropogon scoparius* failed to respond when watered at 42 inches. The last lost 75 percent of its stand in 1936. This was accompanied by smaller but severe losses of Koeleria, *Sporobolus heterolepis, Carex* spp., *Andropogon furcatus,* and Stipa. However, where rainfall was above normal in 1935 and normal up to the time of quadrating (the Hebron prairie) in 1937, *Andropogon scoparius* increased its density by 15 percent. Thus, it is apparent that the fate of this species was controlled by soil moisture at the

TABLE 28. VARIATION IN ABUNDANCE OF MOST IMPORTANT SPECIES IN PERMANENT PLOTS ON ALL PRAIRIES, NUMBER OF PLOTS IN WHICH SPECIES OCCURRED (A), NUMBER OF PRAIRIES ON WHICH SPECIES OCCURRED (B), AND NUMBER OF PRAIRIES ON WHICH SPECIES SUFFERED LOSSES (C)

Species	Number of Stems		Percentage of change	A	B	C
	1936	1937				
GRASSES						
Agropyron smithii	9,187	11,985	+ 30.5	63	9	1
Andropogon furcatus	10,031	7,198	— 28.2	87	9	9
Andropogon scoparius	5,450	1,355	— 75.2	49	9	8
Bouteloua curtipendula	10,140	11,014	+ 8.6	71	9	4
Bouteloua gracilis	20.3*	19.0*	— 6.4	40	8	4
Bromus tectorum	768	3,413	+344.4	32	9	1
Buchloe dactyloides	81.6*	69.4*	— 14.9	14	5	2
Carex	3,625	2,522	— 30.4	74	9	5
Festuca octoflora	(1,248)†	(2,829)†	+126.7	56	8	0
Koeleria cristata	4,902	1,509	— 69.2	57	9	9
Panicum scribnerianum	628	407	— 35.2	46	9	6
Panicum wilcoxianum	737	56	— 92.4	31	9	8
Poa pratensis	10,410	5,448	— 47.7	57	9	7
Sporobolus asper	723	1,045	+ 44.5	25	8	3
Sporobolus cryptandrus	163	283	+ 73.6	16	5	1
Sporobolus heterolepis	1,368	510	— 62.7	16	5	5
Stipa spartea	886	648	— 26.9	18	5	3
NON-GRASSES						
Achillea occidentalis	77	12	— 84.4	9	6	5
Amorpha canescens	517	466	— 9.9	42	9	7
Antennaria campestris	35	23	— 34.3	7	2	2
Artemisia gnaphalodes	1,119	1,045	— 6.6	25	6	5
Aster multiflorus	2,906	2,612	— 10.1	64	9	6
Callirrhoe alceoides	58	87	+ 50.0	12	4	1
Erigeron ramosus	1,031	2,392	+132.0	61	9	2
Hedeoma hispida	290	4,126	+1,322.8	63	8	0
Helianthus rigidus	76	46	— 39.5	13	6	3
Lepidium virginicum	231	3,651	+1,480.5	70	9	0
Liatris punctata	61	28	— 54.1	5	4	3
Linum sulcatum	11	356	+3,136.4	23	6	0
Lithospermum linearifolium	31	43	+ 38.7	17	8	2
Plantago purshii	442	5,635	+1,174.9	29	5	1
Psoralea floribunda	19	30	+ 57.9	11	3	1
Rosa arkansana	40	40	0	9	4	2
Solidago glaberrima	614	538	— 12.4	39	9	5

*Estimated cover in percent.
†Number of square decimeter units in which species occurred.

working depth of its roots, rather than by temperature or humidity. All interstitial grasses sustained general losses. *Panicum wilcoxianum* was nearly wiped out, and *Poa pratensis* was reduced one half, while *Panicum scribnerianum* and *Eragrostis spectabilis* were less affected. Part of the injury to Poa in 1937 was due to the close grazing of grasshoppers. The moisture deficit was so great on the eastern prairies that even the short grasses were unable to hold gains made in 1935 and early in 1936. *Buchloe dactyloides* and *Bouteloua gracilis* were reduced 15 and 6 percent, respectively. Savage and Jacobson (1935) observed that these grasses were considerably injured by drought in 1934, even when aided by artificial watering.

These general losses were partly offset by gains by *Schedonnardus paniculatus* and *Sporobolus cryptandrus* on the western prairies and by general increases of 45 and 30 percent by *S. asper* and *Agropyron smithii*. The latter had spread widely from dense stands on hard, low ground and dust deposits, while *Sporobolus asper* was able to fruit in the absence of the customary late mowing. On the Nelson prairie, where stems of wheat grass were moldy or decayed below ground, an 80 percent loss was recorded. Change in *Bouteloua curtipendula* ranged from a 65 percent loss at Jamaica to a gain of 87 percent at Nelson. The result was a small net increase. The invasion of bared uplands by *Elymus canadensis* from ravines is understandable in the light of its high rate of germination and rapid root penetration (Blake 1935). Stipa was most abundant eastward and absent south and west of Carleton, while *Sporobolus heterolepis* was present only on the 3 prairies nearest Lincoln.

Festuca octoflora was the most abundant and rapidly increasing native annual grass. Its occupancy of square decimeter units rose from 1,200 to 2,800 and the increase in abundance was over 600 percent in plots where stems were counted. It was absent on only one prairie.

Perennial forbs as a group lost 10 percent although small gains were recorded for a few species, for example *Callirrhoe alceoides, Lithospermum linearifolium,* and *Meriolix serrulata* (Table 29).

TABLE 29. TRENDS OF CHANGE IN FLORISTIC COMPOSITION IN PERMANENT PLOTS ON ALL PRAIRIES, NUMBER OF PLOTS IN WHICH SPECIES OCCURRED (A), NUMBER OF PRAIRIES ON WHICH SPECIES OCCURRED (B), AND NUMBER OF PRAIRIES ON WHICH SPECIES SUFFERED LOSSES (C)

	Number	Number of Stems		Percentage of change	A	B	C
		1936	1937				
GRASSES							
Annual	8	1,254	4,612	+267.8	67	9	0
		(1,521)*	(2,423)*	+ 59.3			
Perennial	29	90,088	69,920	— 22.4	98	9	8
FORBS							
Annual	13	1,965	14,544	+640.2	84	9	1
Perennial	42	6,376	5,745	— 9.9	90	0	6
Ruderals	24	1,812	7,913	+336.7	86	9	1
Total	109	100,486	99,500	— 1.0	100	9	5
Bare sq. dm. units	...	(378)*	(402)*	+ 6.3	..	9	..

*Square decimeter units.

By far the most abundant perennial forb, *Aster multiflorus* occurred in 64 of the 100 plots and decreased 10 percent in spite of gains ranging from 1 to 105 percent on the three eastermost prairies. Both Aster and Agropyron are able to take possession of adjacent bare areas very quickly by production of numerous, vigorous, interlacing rhizomes. This habit, together with dissemination of seeds of Agropyron from occasional original areas,

gave this species dominance over considerable territory. Their gains in 1937, however, were limited to areas where over-abundance had not been reached the previous year, and, in general, losses were recorded where they were most abundant in 1936. Thus, it appears that even species favored by drought are subject to control during such periods by the same factors which limit activities of the true dominants.

Although Amorpha gained on two prairies, its general abundance was slightly reduced. The roots of this species penetrate deeply into the subsoil where the moisture-supplying power was low during the summer of 1936, as was shown by the daily folding of the leaves. Under such conditions, photosynthesis is retarded or stopped. That the time of grazing or mowing, as well as their frequency and closeness, influences mortality through its effect on food reserves is well known. Mortality of Amorpha with respect to dates of mowing (as at Carleton) suggests that ability to enter the winter with adequate reserves was the direct contributing factor in survival of this species during drought. Other species showing losses of about 10 percent were *Lygodesmia juncea* and *Solidago glaberrima,* while *Helianthus rigidus, Liatris punctata, Kuhnia glutinosa,* and *Achillea occidentalis* lost 40 to 84 percent. Solidago was severely defoliated by grasshoppers both years. The small, interstitial forb, *Antennaria campestris,* formerly so common, decreased one third on the two prairies where it occurred in plots.

Unlike the perennials, annual forbs and ruderals were sparse in 1936 but formed a dense growth under the favorable conditions of topsoil moisture in the spring of 1937. Hedeoma and Plantago were about ten times more abundant, the former usually interstitial in Agropyron, while Plantago often appeared to take temporary dominance on dry slopes depleted of *Andropogon scoparius* and *Bouteloua gracilis.* In 1935, both seedlings and mature plants of Erigeron were present. In 1936, it was represented mostly by mature plants but in 1937 by seedlings. These, however, made the species 130 percent more abundant than the previous year. Silene was absent in 1936 but abundant on eastern prairies the following year, and seedlings of *Solidago glaberrima* were also common the second year. The clearest annuation was shown by *Linum sulcatum,* which was common in 1935, rare in 1936, and common to abundant in 1937.

Although the prairies were invaded by many ruderals such as species of Amaranthus, Cirsium, Chenopodium, Setaria, and Eragrostis, only two achieved importance. These were Lepidium, which became more abundant on all prairies with increases of 5- to 90-fold, and *Bromus tectorum,* which was present on all prairies and made a 3-fold gain. Tragopogon and Lactuca were important eastward and Salsola westward. Steiger (1930) found that only 4 percent of prairie species were annuals. In 1937, annuals had increased to 19 percent.

That topography has certain strong influences upon plant habitat is well known. It affects temperature, moisture and even soil structure by its influence upon erosion, runoff, infiltration of water, drifting dust and snow, and upon degree and direction of exposure to the wind and sun. As a rule, slopes lose more runoff water than level areas, but the latter are often less pervious owing to the presence of claypan near the surface. North and east slopes may be expected to have lower evaporation rates in summer because of lower insolation and better protection from hot southwest winds. Conditions of drought thus appear most severe on southwest and least on northeast slopes.

Table 30 permits a comparison of three classes of permanent plots, namely, 20 plots on xeric south, southwest, and west slopes, 36 on less xeric north, northeast, and east slopes, and 27 on level ground. The density (number of stems per square meter) of perennial grasses on mesic slopes was higher in 1936 and the loss in 1937 was less than elsewhere. Both lowest density and greatest injury to perennial grasses occurred on level ground, with only slightly less injury on xeric slopes. The scarcity of annual grasses on dry slopes in 1936 and their great increase are correlated with the differences in early season growing conditions. The density of annual forbs was progressively higher from moister to drier slopes in 1936, but the following year they were most abundant on north to east slopes and least on the level. Perennial forbs, which draw chiefly on subsoil moisture, showed both highest density and greatest losses on level ground, while on xeric slopes they made a gain of 10 percent. The weedy *Aster multiflorus* was largely responsible for the gain. Here, too, ruderals were least dense in 1936 and made their largest gains. Total densities on mesic slopes were but little higher than on more xeric ones, while plots on level land contained an intermediate number (1,130) of rooted shoots of all species per square meter. The variation in behavior of a species toward drought on different slopes may depend largely upon the stage of its development and upon its physiological condition, *i.e.* its metabolic preparedness when drought strikes. This, in turn, is determined by the suddenness of the inception of drought and the excellence of prior conditions for growth. A plant which, by virtue of its "favored" position on a north slope, is able to produce a vigorous shoot with minimum development of root hairs and root branches may be unable to adjust itself quickly enough to sudden onset of drought.

Owing to the presence of more available moisture in 1937, the vegetation of all prairies was much taller than the preceding year. The total density of the cover was reduced on the eastern and western prairies but increased on the ones in the southern and central parts of the area where there was more precipitation. An increase in number of bare units per plot was generally accompanied by a decrease in number of species and in total density. The principal invaders of bare areas, in order of decreasing importance, were

TABLE 30. NUMBER OF STEMS PER SQUARE METER AND CHANGES IN FLORISTIC COMPOSITION WITH RESPECT TO TOPOGRAPHY

	Mesic Slopes				Level Ground				Xeric Slopes			
	Average density 1936	Number of Stems		Percentage of change	Average density 1936	Number of Stems		Percentage of change	Average density 1936	Number of Stems		Percentage of change
		1936	1937			1936	1937			1936	1937	
Grasses												
Annual	19.0	565	2,096	+270.0	36.2	800	1,900	+137.5	0.6	10	149	+1,390.0
	*(24.8)	*(737)	*(1,125)	+ 52.6	*(19.3)	*(426)	*(680)	+ 59.6	*(15.0)	*(247)	*(391)	+ 58.3
Perennial	1,112.6	33,045	28,096	— 15.0	960.2	21,220	16,341	— 23.0	1,055.7	17,420	13,512	— 22.4
Forbs												
Annual	20.9	622	8,758	+1,308.0	23.4	518	1,473	+ 184.3	31.1	514	2,260	+339.5
Perennial	57.5	1,718	1,495	— 13.0	93.7	2,072	1,561	— 24.6	75.9	1,253	1,375	+ 9.7
Ruderals	14.3	426	2,450	+475.1	51.2	1,139	3,131	+174.0	8.4	138	973	+605.1
Total	1,181.1	35,079	42,049	+ 19.9	1,130.3	24,979	23,391	— 6.4	1,170.8	19,318	18,343	— 5.0
Bare sq. dm. units	*(5.9)	*(176)	*(120)	— 31.5	(3.2)	*(71)	*(139)	+ 95.8	*(6.1)	*(101)	*(103)	+ 2.0

*Square decimeter units.

Festuca, Hedeoma, Lepidium, *Bouteloua curtipendula*, and Agropyron. Similarly, the species whose death caused bare areas were Poa, *Andropogon furcatus*, Erigeron, *Bouteloua curtipendula*, and *Andropogon scoparius*. *Bouteloua curtipendula* thus appears to have been the most unstable of the perennial grasses.

Investigations of soil reaction, chloride and moisture contents did not disclose the reasons for the sharp and prevalent alternation shown by perennial grasses. It must be kept in mind, however, that the supply of available soil moisture was abnormally low during this study. That such a study would throw light on the question of the causes of alternation if carried out at weekly intervals during a normal period is not unlikely. Cain (1931) found that contiguous forest communities could not be separated on the basis of reaction alone. Emmett and Ashby (1934) applied statistical methods to show that for Pteridium and Vaccinium there is no optimum pH within their pH range. This may well be true also for prairie grasses.

The range in soil moisture content at a depth of 2 feet was greater, that is higher and lower, under *Andropogon furcatus* than under any other type, while near roots of *Bouteloua gracilis* less moisture with a narrower range was the rule. Soils of unlike structure and permeability were found to differ markedly as to their vegetative cover.

Wheat grass was commonly the dominant on deeper deposits of dust and on shallow soils underlain by claypan. Particles of drifted soil sometimes become very firmly cemented into a brick-like layer. This is probably due to the presence of an excess of colloidal material. Fly (1935) reports that both dust and drifted soil had a higher percentage of total colloids than was present in normal surface soil. For this reason, the rate of infiltration of water into the soil in wheat-grass alternes was measured in hours rather than in minutes as in other types of vegetation. No marked difference in rate of penetration by water was found between undisturbed bare soil and vegetated soil close at hand. Soil ramified by fine, fibrous root systems was neither more nor less pervious than that penetrated by large, deep taproots such as those of *Liatris punctata*, *Amorpha canescens*, and *Rosa arkansana*. These results are not in agreement with those of Pearse and Woolley (1936), who used different equipment and a procedure which involved the flowing of a thin sheet of water over sloping ground and brought into play the damming action of the vegetation. However, Musgrave and Free (1936), who used the cylinders, found that neither alfalfa nor bluegrass increased infiltration enough to account for their effectiveness in reducing runoff. Infiltration into the loose, granular soil characteristically occupied by the sod form of big bluestem was consistently more rapid than into soil of the 11 other types tested. Dead crowns failed to absorb even the first two inches as quickly as big bluestem. Whether grasses, such as big bluestem and wheat grass, have the ability to change the structure of the soil or whether they

merely are better adapted to loose and hard soils, respectively, remains to be shown.

Although the sod-forming grasses have been badly depleted by drought, little erosion by water is likely to occur on prairie slopes. That the soil is unusually high in decaying plant material was indicated by the abundance of certain saprophytic fungi, notably *Simblum sphaerocephalum*. In addition, numerous rapidly growing annuals quickly clothe areas bared by death of perennials. Composite shallow soil samples taken at random from each of 5 prairies yielded seedlings of 42 species during 5 months of care in the greenhouse. Annuals constituted 34 of the species and 92 percent of the seedlings, most of which appeared the first month. Six-weeks fescue was by far the most abundant species.

SUMMARY

The drought of 1936 continued the destruction which in 1934 so greatly changed the composition of native vegetation of the true prairie. The summer of 1936 was the hottest and driest ever recorded in eastern Nebraska.

Studies were made of 100 permanent list plots, together with estimates of abundance of all species occurring in randomly selected temporary plots on nine annually mowed, but ungrazed, prairies in 1936 and 1937.

Perennial grasses were reduced in abundance 22 percent, perennial forbs 10 percent. Annual forbs, ruderals, and grasses were 3 to 6 times more abundant in 1937 than in the preceding year. Big bluestem was reduced 28 percent in abundance and 20 in percentage occurrence. Similarly, little bluestem lost 75 and 68 percent; blue grama, 6 and 9 percent; June grass, 69 and 43 percent; and Kentucky bluegrass, 48 and 57 percent. Western wheat grass increased 30 percent in abundance and side-oats grama over 8 percent. The corresponding increases in percentage occurrence were 36 and 100 percent. The total density of the vegetation remained nearly constant in the permanent plots, since annuals replaced the perennials.

The increase of 6 percent in number of bare square decimeter units of observation in permanent plots was due largely to disappearance of *Poa pratensis, Bouteloua curtipendula, Andropogon furcatus,* and *Erigeron ramosus.* Among the invaders of bared units, Festuca, Hedeoma, *Bouteloua curtipendula,* and Agropyron ranked foremost.

Greenhouse care of composite random samples of bare surface soil secured in August, 1937, showed that seeds of 8 perennial and 34 annual species were present. Annual plants constituted 92 percent of the population.

There was an increase of 5 percent in the number of species per plot (13.1) in spite of consistent losses of perennial grass species. Perennial forbs were inconsistent but annual grasses, annual forbs, and ruderals, almost without exception, made gains.

The general height of the vegetation was greater in 1937 in response to a supply of moisture which was more nearly normal than in 1936. No dwarfing occurred which could be attributed to drought injury received the preceding year.

Slope exposure had a marked influence on behavior toward drought. Perennial grasses were more dense and suffered a lower loss on mesic slopes than on xeric slopes or on level ground. Long-lived forbs were most dense and most injured on the level but they gained 10 percent on xeric slopes. Other factors than slope exposure which modified the effects of drought were deposition of drifting soil and alluvium, burning, hail, grasshoppers, variation in previous dates of mowing, and variation in permeability of the soil to water.

The widest range in soil moisture content was found in big bluestem, while soil occupied by blue grama had a lower average content and a narrower range. No consistent relationship could be found between any kind of alterne and the chloride content, carbonate content, or pH of the soil underlying it. However, the rate of infiltration of water into the soil in certain types of vegetation was characteristic. Steel cylinders 4 inches in diameter were pressed into the soil to a depth of 14 inches and 4 inches of water were added, one at a time, to the inch of cylinder remaining above the surface of the soil. Big bluestem soil absorbed most readily and the soil occupied by wheat grass least rapidly of the twelve types measured. Large taproots did not differ from fine, fibrous ones in their influence on the rate of infiltration when the damming action of the vegetation was barred.

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POLLEN SPECTRUM STUDIES ON THE ANOKA SAND PLAIN IN MINNESOTA

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POLLEN SPECTRUM STUDIES ON THE ANOKA SAND PLAIN IN MINNESOTA

INTRODUCTION

Pollen-analytical studies of single bogs in widely distributed localities undoubtedly provide valuable records of postglacial forest succession. It would seem, however, that conclusions as to vegetational and climatic progression drawn from data on a single bog may be unreliable since it is impossible to know whether the bog investigated represents the rule or an exception. It appears obvious that for a given locality a study of a group of bogs should give more valid results. Such group studies have only recently been undertaken. Voss (1934) has investigated seven bogs in Lake County, Illinois; and later (1937), nine on older moraine in Bureau County, Illinois. Wilson (1938) has compared fossil spectra of ten bogs in Douglas County, Wisconsin, to determine the vegetational history of that region.

The present study was planned first of all, naturally, as a new contribution to the knowledge of forest and climatic succession during postglacial time in North America. The group method was adopted in order to determine whether this is sufficiently more reliable than the single-bog plan, unavoidable in reconnaissance studies, to justify the far greater amount of labor involved.

Collection of peat and marl samples from bogs on the Anoka Sand Plain, in east-central Minnesota, was begun in the spring of 1935, and field work was carried on at intervals until the autumn of 1937. The Anoka Sand Plain was selected because, in addition to offering a wealth of material, it is a distinct and homogeneous physiographic unit, whose origin and history have been carefully worked out (Cooper, 1935).

HISTORICAL SUMMARY

Many European students have attempted to work out by the method of pollen analysis the forest history of Europe during postglacial time. Marked changes in forest composition shown in the profiles have been assumed to be the direct result of changes in climate. The latest workers favor the climatic schedule of Von Post (1930), who has divided postglacial time into three periods, of increasing, maximum, and decreasing temperature, respectively.

American workers, using the methods evolved by the Europeans, have endeavored to reconstruct the postglacial forest sequence on this continent, and to discover whether, and to what extent, it runs parallel to that of Europe. Studies in eastern North America, mainly within the glaciated region, show that the record in practically all bogs begins with an overwhelming percentage of Abies and Picea pollen. In the upper two thirds of the profiles important regional differences appear, which will be briefly described.

In southeastern Canada (Auer, 1930), northern Wisconsin and Minnesota (Voss, 1934), dominance of Abies and Picea is replaced by that of Pinus, which is abundant throughout. There is a slight indication of deciduous dominance in the middle third of some profiles. In the upper layers, Abies and Picea again increase at the expense of Pinus.

Profiles from central Wisconsin (Voss, 1934), Michigan (Potzger, 1932) and northern Indiana (Houdek, 1933; Lindsay, 1932) are similar except for a definite middle period of deciduous dominance instead of a mere suggestion.

In Ohio (Sears, 1932), central Indiana (Houdek, 1933; Prettyman, 1937; Smith, 1937; Barnett, 1937) and northern Illinois (Voss, 1934), following the conifers, deciduous dominance is marked and extends to the present. Pine is usually abundant throughout.

In Iowa (Lane, 1931), conifers are rapidly replaced by deciduous genera and these in turn quickly give way to grasses. An Amaranth-Chenopod maximum appears at the 4-foot level but above this grasses again become dominant.

As to interpretation, there is general agreement among investigators that the universal and rather abrupt early change from fir-spruce to pine-deciduous dominance was due to change in climate, in which rise of temperature was an important element. With regard to the upper two thirds of the profiles, two divergent views are held. The first asserts that marked fluctuations in pollen frequency of the most significant genera are direct indications of widespread changes in forest composition due to climatic changes. The second, recently put forth, maintains that the observed facts are more reasonably explained on the basis of local ecological processes such as succession.

Statements supporting the first view have been made by several workers. In summarizing results from pollen analysis in eastern North America, Sears (1935b, p. 498) concludes that "the simple schedule of Von Post . . . is broad enough to allow of future refinement, and does no violence to the facts." The first period of increasing warmth is probably to be correlated with the rapid decline of the northern conifers and the advance of the deciduous forest. Concerning the second stage, Sears states that the "evidence indicates a period of maxium warmth and probably, dryness, now past" (1935b, p. 497). The nature of this evidence, according to Sears, is of several kinds: (1) dominance of oak in the middle of the profiles from Minnesota and southeastern Canada and its subsequent retreat; (2) an oak-hickory maximum at the 11-foot level in the combined profile of two Ohio bogs and (3) an Amaranth-Chenopod maximum at the 4-foot level in a bog in Iowa. The term "xerothermic" has been applied to this theoretical period of maximum warmth. As evidence for the third climatic change, Sears points to the "general recent increase of spruce at the northern stations. Southward it appears in the form of general evidence of increasing meso-

phytism—more Acer, Fagus, Liquidambar, and southern pine" (1935b, p. 497).

Fuller (1935) divides the postglacial forest succession of the Lake Michigan region into three stages, viz: (1) a period of establishment and relatively rapid decline of the northern conifer type, indicating an interval of increasing warmth; (2) a long period of dominance of deciduous forests, indicating a period of maximum warmth; (3) a poorly marked, rather short period of slight increase in the boreal types indicating a period of decreasing warmth.

Hansen (1937) considers that this same sequence is borne out in profiles from his two Wisconsin bogs, one located within and the other adjacent to the Driftless Area. In the former, pollen of spruce and fir is predominant in the lowest level while in the latter the record begins with the dominance of pine. A very brief period during which oak is dominant appears in the middle portions of both spectra and is considered to be correlated with the period of maximum warmth. A sharp decrease in the frequency of pine and sedge at the 7-foot horizon in both bogs and an increase in composites and grasses at the same level in the Driftless Area deposit may indicate a xerothermic period (1937, p. 148). Concerning the upper third of the profiles, Hansen says: "There seems to be no definite increase in the boreal types in the last period, but a slight decrease is shown in the deciduous trees since they reached the maximum during the second period" (1937, p. 148).

Other workers interpret the same profiles differently or put forward new evidence to support the second view stated above. The interpretation which Voss (1934) has placed on his own profiles from Minnesota, Wisconsin, and Illinois is the converse of the view held by Sears and Fuller. He states: "The northern bogs, Coleraine and Highland in Minnesota . . . show that the type of vegetation has remained practically the same throughout their development" (1934, p. 39). Conifers have been the significant trees during the entire history of the bogs. He concludes, therefore, that no climatic fluctuations are indicated by the pollen diagrams of the bogs located upon drift of Substage IV of the Wisconsin Period (1934, p. 40).

The recent increase of spruce in profiles from the northern stations is considered by Sears and Fuller to indicate a return to a cooler climate. Voss, however, believes that "In the Waupaca and Hayward bogs in Wisconsin . . . the increase of Picea near the surface may be due to the presence of the bog spruce *(P. mariana)* on the surrounding mature bogs" (1934, pp. 10-11). Moreover, in summarizing his work on central Wisconsin and northern Illinois bogs, he says: "The pollen diagrams . . . indicate that conditions remained very uniform during the period represented by the upper two thirds of the diagrams" (1934, pp. 39-40). He therefore considers that no climatic fluctuations are proven in profiles of bogs found upon drift of Substage III of the Wisconsin Period.

More recently, in profiles from nine bogs located on Tazewell drift in

Illinois, Voss (1937) again finds no evidence supporting the theory of a xerothermic period during postglacial time. The succession of forests as shown by the pollen diagrams is: (1) increase and dominance of the conifers, (2) decline of the conifers and advance of the deciduous forest.

Wilson (1938) has reported on ten bogs related to shorelines of glacial Lakes Duluth, Algonquin, and Nipissing in Douglas County, Wisconsin. The fossil spectra indicate that upon each area of land that was progressively uncovered by the waters of the glacial lakes there developed a pioneer forest of Picea. This was variously replaced by pine and hardwood forests in response to the soils of the county. Throughout the profiles, there are two levels in which Picea is of marked importance: first, at the bottom; and second, at or near the top. Although a climatic significance has been attributed to this type of curve by other workers, he maintains that such a curve is also easily explained by local succession of trees upon the bogs. The second increase in Picea fossils has been shown to be contemporaneous with the transition of peat from limnic to subaerial (Wilson and Galloway, 1937).

GEOLOGY

Since the origin of the Anoka Sand Plain is closely correlated with the last of the ice lobes that invaded Minnesota during the glacial epoch, a review of the ice movements of the Wisconsin Period seems pertinent. According to Leverett (1932, pp. 39-55), the advance in Middle Wisconsin time was a movement across the state which reached a point near the present sites of Minneapolis and St. Paul. It has been designated, therefore, as the Minneapolis Lobe of the Patrician Ice Sheet (Cooper, 1935, p. 6). The young red drift deposited by this ice lobe is a sandy or loamy till containing rock fragments of all kinds and sizes. The visible result of this ice invasion is a terminal deposit of unusual strength and continuity, the St. Croix Morainic System (Leverett and Sardeson, 1932, pp. 39-42).

While the Minneapolis Lobe was still present within the state but distinctly on the wane, two new ice lobes invaded the region. One, the Superior Lobe of the Labrador Ice Sheet, traversed the basin of Lake Superior and reached a point in Minnesota sixty miles southwest of Duluth. The other and larger body was due to an ice advance southeastward from the Keewatin center in central Canada. It covered most of southeastern Minnesota and spread southward as far as Des Moines, Iowa, from which city it takes its name (Leverett and Sardeson, 1932, p. 56). The young gray drift of Minnesota and neighboring parts of the Dakotas and Iowa was deposited by this ice sheet. It is characterized by an abundance of limestone, fine silt and clay, and few boulders.

The origin of the Anoka Sand Plain has been described by Cooper as follows (1938): "The history of the Anoka Sand Plain is a complex one. When the Minneapolis Lobe of the Patrician Ice Sheet shrank away from its line of maximum extension it left behind a terminal accumulation of

unusual strength and continuity, the St. Croix Morainic System. The main drainage channel taking the meltwater from the west side of the receding ice edge became established between the morainic belt and the ice, following approximately the present course of the Mississippi southward from the vicinity of Brainerd to St. Cloud, and thence southeastward, still parallel to the moraine and just within it, to the apex of the lobe.

"Very soon—probably while stagnant remnants of Patrician ice still lingered in the vicinity—the Des Moines Lobe of the Keewatin Ice Sheet advanced from the northwest. From Brainerd to St. Cloud the area just vacated by Patrician ice was barely touched by this invasion, but between St. Cloud and Minneapolis, a strange extrusion from the Des Moines Lobe, the Grantsburg Sublobe, overrode the St. Croix Moraine and spread northeastward a distance of 130 kilometers.

"The trunk stream flowing within and parallel to the moraine was of necessity forced out of its course and compelled to skirt the advancing edge of the ice. At maximum extension the Sublobe made contact with relatively high land in Wisconsin, completing the encirclement of an extensive lowland and thus causing the appearance of Glacial Lake Grantsburg. Recession or disintegration of the Grantsburg Sublobe brought first of all drainage of the lake, and then a slow return of the Mississippi to its former course."

The further history is given in more detail by Cooper in an earlier publication (1935). ". . . the drainage from the west and northwest, which at the maximum had emptied into Lake Grantsburg, now skirted the ice edge as a glacial river of great size, which wore back the margin at a rapid rate. Often it encountered gaps in the continuity of the disintegrating ice sheet, and portions of its waters flowed through them, accelerating its disappearance and building up sedimentary deposits en route. With continued thinning of the ice, the waters came to flow in places over its surface, burying extensive masses beneath a load of sand and gravel. During the process, great expanses must have appeared as a chaotic maze of ice-blocks, sediment-laden watercourses and unstable sand flats.

"With all this confusion there was a definite progressive shift in the path of the waters. The general subglacial surface was toward the south, and accordingly, as the northern margin receded in its irregular fashion, the skirting streams followed it, subject to frequent interference due to projecting morainic masses.

"The visible result of all these activities is a great outwash plain that covers a large part of the territory occupied by the Grantsburg Sublobe (Fig. 1). It is of an unusual type—not in any sense an apron derived from materials contributed directly by the adjoining ice, but built entirely of sediments brought from considerable distances by a great river, flowing across an area only partly vacated by local ice. . . . It may be called the Anoka Sand Plain from the county in which it is most largely developed."

The total area of the plain, excluding the morainic masses occurring within it, is about 850 square miles. It occurs principally in four counties: Anoka, Isanti, Sherburne and Chisago. Its outer edges extend into portions of Mille Lacs, Ramsey and Washington counties.

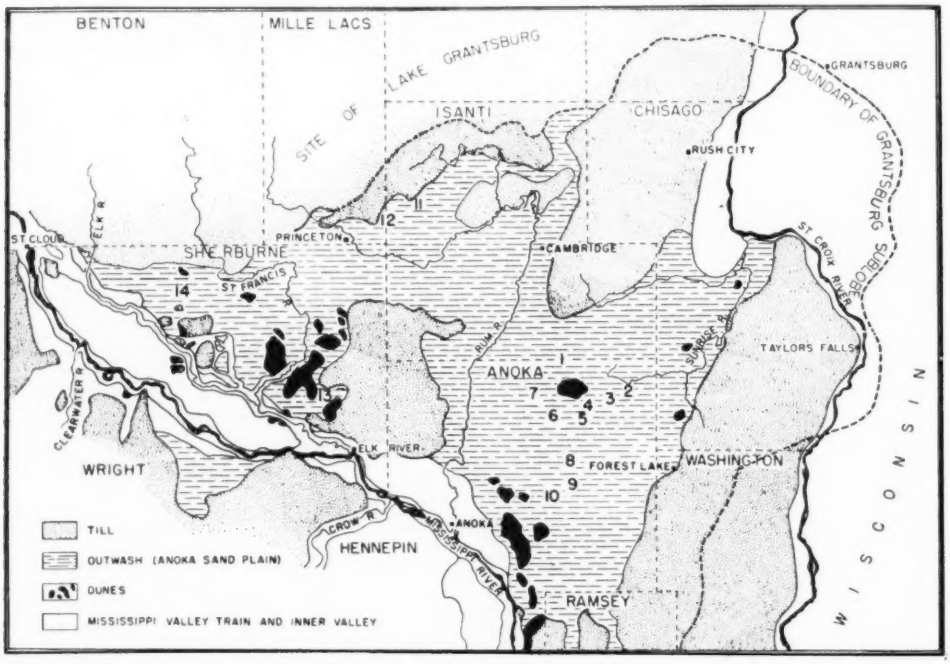

FIG. 1. The Anoka Sand Plain, showing its relation to adjoining physiographic units and location of bogs studies. (After Cooper, 1938.) 1. Cedar Creek; 2. Tamarack Lake; 3. Rabbit Lake; 4. Linwood; 5. Rice Lake; 6. Grass Lake; 7. Bethel; 8. Coon Lake; 9. Coon Creek; 10. Ham Lake; 11. Karmel; 12. Princeton; 13. Elk River; 14. Clear Lake.

"The surface of the plain in various portions is practically flat, gently rolling, sharply rolling, or plateau-like with pits. Pits of all sizes occur, ranging from small shallow sags to depressions a mile or more in extent. Many are occupied wholly or in part by ponds or lakes. Peat deposits are numerous, some of them having a thickness of 15 feet and more. The pit bottoms, where not floored by peat, are mostly irregularly rolling" (Cooper, 1935, p. 45).

Detailed analysis of the materials of the sand plain shows that they are mainly composed of fine and very fine sands (Cooper, 1935, p. 46). While the ice was retreating from the area, the sand must have been saturated with water. Gradual lowering of the water table, brought about by downcutting of the Mississippi and its tributaries, made conditions favorable to invasion by plants. Cessation of downcutting brought stabilization of the water levels. The depressions still filled with water remained as lakes or ponds suitable to colonization by peat-forming species. Certain of the resulting bogs furnish the materials for the present investigation. All of those selected lie within

the boundaries of the sand plain itself—none upon the surrounding till have been considered. All have thus had an essentially similar physiographic history.

LOCATION OF BOGS

The locations of the fourteen bogs in which pollen analyses were made are shown on the map (Fig. 1).

1. Cedar Creek bog is a tamarack and white cedar bog in the center of which a small body of open water still remains, surrounded by a quaking mat about 50 yards wide. At the water's edge there is a discontinuous zone of wild rice (*Zizania aquatica* L.) and water willow (*Decodon verticillatus* (L.) Ell.). It is about 4 miles northeast of the town of Bethel, in the northeast quarter of Section 27, T.34 N., R.23 W., Anoka County.

2. Tamarack Lake occupies part of the southwest quarter of Section 4, T.33 N., R.22 W., Anoka County. It is an extensive and deep peat-filled lake with a quaking mat which will scarcely support a man's weight. There are no trees on the surface and the mat consists of grasses, rushes and sedges.

3. Rabbit Lake, in the northwest quarter of Section 5, T.33 N., R.22 W., Anoka County, is a quaking tamarack bog with open water in the center. It appears on the soil map of the county (Smith *et al.*, 1918) as a small open lake but is now almost completely covered over by the sedge mat.

4. Linwood bog lies in a deep ice-block pit and has a stable surface covered with tamarack, Sphagnum and a few ericads. It is located near the town of Linwood on the property of Clifford Carlisle in the northeast quarter of Section 8, T.33 N., R.23 W., Anoka County.

5. Rice Lake is also shown on the soil map as an extensive lake but is now practically covered by a quaking mat of grasses and sedges. It is in Bethel Township, in the northeast quarter of Section 24, T.32 N., R.23 W., Anoka County.

6. Grass Lake, about two miles southeast of Bethel, occupies most of the northeast quarter of Section 10, T.33 N., R.23 W., Anoka County. It is a shallow peat-filled lake of the bog meadow type overgrown with grasses and sedges.

7. Bethel bog is located beside Highway 65 about 1.5 miles south of Bethel in the northeast quarter of Section 5, T.33 N., R.23 W., Anoka County. It lies in a shallow ice-block pit and the peat is now completely covered with a luxuriant growth of leatherleaf (*Chamædaphne calyculata* (L.) Moench.).

8. Coon Lake is the only spruce-tamarack bog investigated and is located southeast of Coon Lake in Section 36, T.32 N., R.23 W., Anoka County. The principal vegetation consists of tamarack (*Larix laricina* (DuRoi) Koch.), black spruce (*Picea mariana* (Mill.) BSP), *Sphagnum* spp., Labrador tea (*Ledum groenlandicum* Oeder.), and red-osier dogwood (*Cornus stolonifera* Michx.).

9. Coon Creek bog is situated in a deep depression and has a non-quaking mat on which the principal trees are tamarack, white pine (*Pinos strobos* L.) and paper birch (*Betula papyrifera* Marsh.). Its location is Section 26, T.32 N., R.23 W., Anoka County.

10. Ham Lake bog is mature and the important trees are the same as in the Coon Creek deposit. It occurs southeast of Ham Lake in Section 21, T.32 N., R.23 W., Anoka County.

11. Karmel bog, so named by the writer because of its proximity to the town of Karmel, is a mature bog located in the southwest quarter of Section 3, T.36 N., R.25 W., Isanti County. The principal vegetation on the mat consists of tamarack, white pine, large-toothed aspen (*Populus grandidentata* Michx.), quaking aspen (*P. tremuloides* Michx.) leatherleaf, and bog birch (*Betula pumila* L. *var. glandulifera* Regel.).

12. Princeton bog is located 6 miles northeast of the town of Princeton in the southeast quarter of Section 13, T.36 N., R.26 W., Mille Lacs County. It appears as a small oval depression surrounded by ridges of sandy outwash. The bog had been opened to pasture but the principal woody plants, tamarack and speckled alder (*Alnus incana* (L.) Moench.) still remained.

13. Elk River bog is located 7.5 miles northwest of Elk River in the northwest quarter of Section 5, T.33 N., R.27 W., Sherburne County. The deposit is deep and the peat is stable, upon which the following plants were noted: tamarack, paper birch, elm (*Ulmus americana* L.), red-osier dogwood, raspberry (*Rubus strigosus* Michx.), bush honeysuckle (*Diervilla Lonicera* Mill.) a sedge (*Carex comosa* Boott.), speckled alder, royal fern (*Osmunda regalis* L.) and cinnamon fern (*O. cinnamomea* L.).

14. Clear Lake bog is densely covered with tamarack, white pine and paper birch. It is a peat deposit occupying a depression in the sand plain, located 7.5 miles northeast of the town of Clear Lake in the northeast quarter of Section 23, T.35 N., R.29 W., Sherburne County.

METHODS

Erdtman (1931) has outlined a method whereby the earliest sediments in a bog may most likely be obtained. Preliminary drillings are made to determine the deepest portion of the bog, and at this point a single series of samples is taken at regular intervals from the surface to the bottom. This procedure was followed in the present study. There has been some controversy among bog pollen workers as to whether a single section gives a pollen spectrum typical of the entire bog. Sears (1930) has shown, from results of four borings in an Ohio bog, that considerable fluctuation does occur at corresponding levels in different parts of the same bog, but that the principal trends are equally clear in all sections. Recent studies of three bogs in each of which two drillings were made (Prettyman, 1937; Smith, 1937; Barnett, 1937) gave pollen profiles which were essentially similar.

In the present investigation, therefore, it seemed advisable to make single drillings in a large number of bogs rather than to carry on more detailed studies in a single one, as was done in a previous study (Artist, 1936). Samples of peat used for the microscopic analysis were collected at 20 centimeter intervals from the surface to the bottom by means of a peat sampler of the cylindrical type, a modification of the Swedish instrument used by Auer (1930). It consists essentially of a cylinder approximately 2.5 centimeters in diameter and 40 centimeters in length with a cutting edge which can be opened or closed by rotating the handle of the instrument. The peat is collected in a removable chamber which fits snugly inside the steel outer cylinder. Fifteen detachable one-meter rods were available, and these were marked off into 20 centimeter lengths for determining the depth of sampling.

In all cases except one the peat or marl was found to rest upon sand; in Cedar Creek bog the bottom was not reached. As a precaution against contamination the samples were removed from the center of the core and quickly placed in numbered double-ended glass vials. The peat chamber was thoroughly cleaned after each sample was removed. Notes were taken on the general physical character of the materials collected and the complete series of samples were brought into the laboratory and prepared for the microscopic analysis in their natural state of wetness.

During the first part of the work, the procedure outlined by Wilson and Galloway (1937, p. 114) was followed in preparation of the peat for pollen counts. This method differs from the usual alkali technique in that distilled water only is used and the peat is allowed to stand in glycerine jelly in a desiccator for 24-48 hours. The amount of time consumed in removing any traces of water from the material to be mounted was found to be the main difficulty; otherwise, the method gave good results.

A number of other methods employed by various workers in pollen analysis (Sears, 1930; Voss, 1931; Potzger, 1932) were tried at some time during the course of the work, particularly the acetic anhydride treatment of Erdtman (1936) and the alcohol method of Geisler (1935). Erdtman's method entails an added amount of work with results but little better than can be obtained by a simpler technique, and that of Geisler was found to work well only when the pollen content of the peat was reasonably high. All these methods were given a fair trial but the procedure employed throughout the greater part of the present investigation gave the best and most consistent results and required little time.

A quantity of peat was placed in a 100 cc. beaker, a sufficient amount of warm water to cover it was added and the material carefully broken up with the finger by pressing against the sides of the vessel. About 10 cc. of a one percent solution of NaOH was added and the material was warmed, care being taken that it did not come to the boiling point at any time. If the peat was very coarse and fibrous, it was strained through a 1 mm. copper

sieve to remove most of the debris. Examination of peat on test slides before and after straining revealed that surprisingly few of even the larger pollen grains were retained by the sieve. Enough safranin was added to color the liquid deeply, which was then centrifuged. The tip of a scalpel was used to remove a small amount of the material from the surface of the sediment in the centrifuge tube and to transfer it to a few drops of glycerine jelly on a cover slip which was then inverted onto a slide. Test slides were observed to determine in a general way the pollen frequency of the peat, which gave a rough measure of the necessary number of slides to be made. After cooling, the mounts were ready for counting under the microscope.

Samples of marl were treated with concentrated hydrochloric acid to remove calcium carbonate. After the liquid had ceased to effervesce, the acid was washed out with water by centrifuging. The material was stained with safranin, again centrifuged and mounted in the manner described above. Without acid treatment of marl samples, it was difficult and often impossible to make out the finer details of the pollen grains due to masking by the finely divided carbonate.

Identification of the fossil pollen was made by comparing with prepared slides of present-day pollen of the same genera. Pollen grains and spores of herbarium specimens and living plants were treated with NaOH and stained with safranin to simulate peat material. The works of Wodehouse (1935) and Sears (1930) were also helpful in the identification.

A Leitz binocular microscope equipped with 10x oculars, condenser and a graduated mechanical stage was used in making the counts and identifying the pollen. In the first part of the work, 50 pollen grains on each of four slides were counted for each sample, the percentage being computed from a total of four. As the work progressed, it was found that with peat in which the pollen frequency was fairly high a count of 200 on a single slide gave equally good percentages. Many comparisons were made of relative percentages obtained from counts of 100 and 200, and, as Potzger (1932) has shown, there were no significant differences. It is noteworthy that counts of 50 pollen grains on each of four slides for every sample were practically identical. All established the same relative percentage for the most abundant genera, but if only one slide was counted, infrequent pollen grains appearing in counts of 100 were often entirely absent. Throughout most of the work in the present study, therefore, 100 grains were counted. The absolute pollen frequency, or number of pollen grains per square centimeter of slide material, was also determined.

RESULTS

Results of microscopic analyses of peat and marl samples from fourteen bogs on the Anoka Sand Plain are shown in the form of tables (1 to 15) and diagrams (Figs. 2 to 16). Only the curves of the most significant genera

are included in the pollen spectra. These are: Abies, Picea, Pinus, and Quercus. The pollen frequency percentages of the trees and shrubs not shown in the diagrams and of the families Compositæ, Gramineæ, Nymphæaceæ, and of Amaranth-Chenopod genera considered together are given in the tables.

SEQUENCE OF PEAT LAYERS

Field observation shows two types of bogs: the extensive, treeless sedge-grass marshes and the comparatively small and deep tamarack, white cedar or spruce bogs, the so-called muskegs (Soper, 1916, p. 56). Examination of peat samples in the laboratory, however, shows that the sequence of peat layers is generally similar in bogs of the two types.

A generalized profile would include two distinct types of peat: (1) *limnic peat*, a layer varying in thickness from 0.2 meter to almost 4 meters, usually resting upon the sand bottom; and (2) *carex peat*, always above the first, of varying thickness, in some cases making up nearly the whole section. An additional layer of non-shell marl underlies the limnic peat in five of the bogs (Figs. 5, 6, 9, 10, 12); in two this makes a considerable part of the section.

There are three exceptions to such a generalized profile. In Cedar Creek bog (Fig. 10), *Sphagnum peat*, not more than twenty centimeters in depth, occurs over an extremely deep deposit consisting of 8 meters of non-shell marl, 0.8 meter of limnic peat and 2.2 meters of Carex peat. Linwood bog (Fig. 4) has a layer of *Sphagnum peat* 3 meters in thickness above the usual sequence of limnic and Carex peat layers. The surface of Coon Lake bog (Fig. 3) in the area of sampling was found to be a coarse, fibrous and woody peat layer made up largely of branches and roots of trees and shrubs about 0.2 meter thick.

The peat designated as limnic consists of sedimentary organic matter deposited under water. Wilson and Galloway (1937) consider as characteristic of this type such fossils as pollen and internal leaf trichomes of water lily, barbed and plain sponge spicules and diatoms. Carex peat is a general term for plant remains of the sedge-grass type, finely fibrous, dark brown to black, rarely containing the fossils noted above.

Comparison of pollen spectra

Comparison of the fourteen pollen spectra shows at once certain features common to all (Figs. 2 to 15). However, on the basis of the kind of pollen dominant in the lowest levels, the spectra may be divided into two main groups, characterized as follows:

Group I includes ten bogs in which pollen of Abies and Picea is most abundant at the bottom. In five of these profiles (Figs. 2, 3, 4, 5, 6) initial dominance of Abies is followed by dominance of Picea, while in the remaining five (Figs. 7, 8, 9, 10, 11) Picea dominates first and is succeeded by Pinus, Abies being present in but minor amount.

Group II comprises four bogs in which, regardless of depth, no Abies or Picea maximum occurs in the bottom peat or marl, the earliest record beginning with dominance of Pinus and Quercus (Figs. 12, 13, 14, 15).

The spectrum most typical of each group will be described in detail. Discussion of other profiles will be limited to brief comparison with the type. The number following each bog refers to its location as indicated on the map (Fig. 1).

GROUP I. PROFILES BEGINNING WITH DOMINANCE OF ABIES AND PICEA

Coon Creek-bog (10; Table 1, Fig. 2) may be considered the type of five bogs which show the complete fossil succession of the region. The record begins with an overwhelming dominance of Abies pollen which comprises almost 90 percent of the total number of pollen grains counted at the lowest level. Picea and Pinus are present only in minor amount. It should be noted that Quercus pollen occurs very early in the history of the bog, first appearing at the level immediately above the bottom. The curve of Abies declines rapidly and Picea becomes the dominant pollen at 6.6 meters, later reaching a maximum of 61.5 percent at the 6.2 meter level. Picea, in turn, decreases rapidly and gives way to a Pinus maximum of 90 percent at 5.2 meters. Pollen of Abies disappears from the lower part of the diagram at 5.8 meters, while Picea continues, although in steadily decreasing amounts, to the 5-meter level. The latter occurs sporadically at higher levels, often accompanied by lesser amounts of Abies.

Quercus attains its initial dominance at the 4.4-meter mark but is only slightly more abundant than Pinus. From this point upward, the curves of these genera show considerable fluctuation, crossing and re-crossing as one attains a maximum at the expense of the other. The relative pollen frequency of any one kind of pollen affects the percentages of all the others, and therefore, where there is an increase in Quercus pollen, there must be a corresponding decrease in percentage of Pinus.

Pollen of Betula, Alnus and Corylus (Table 1) is infrequent until the upper layers are reached. The birch pollen may be from the paper birch (*Betula papyrifera* Marsh.) or from the bog shrub (*B. pumila* L. var. *glandulifera* Regel) both of which may have grown upon the adjacent uplands in the earliest times. The increase in Betula pollen near the surface may be correlated with the relatively late appearance of the latter species on the sedge mat. Ulmus appears early in the spectrum and reaches a frequency as high as 12.5 percent at the 4.8-meter level. Pollen of Juglans, Tilia, and Acer is rare and scattered through the section. A single pollen grain of Carya was found at the 4.8-meter level—the only one observed throughout the entire investigation. Pollen of Compositæ, Gramineæ, and of Amaranth-Chenopod type is abundant throughout the profile in comparison with other angiosperms except Quercus. An increase in pollen of Nymphæaceæ

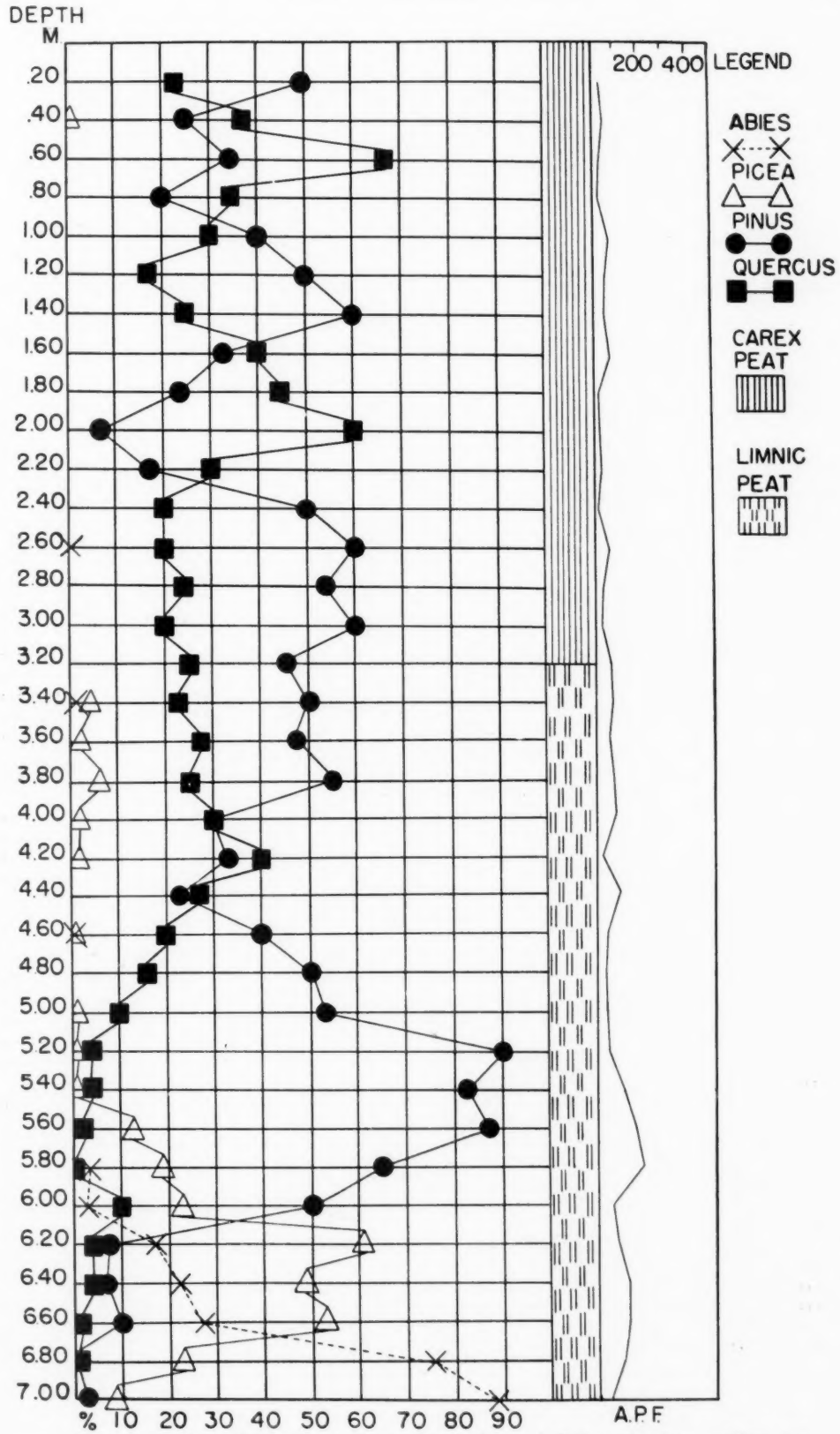

FIG. 2. Pollen diagram of Coon Creek bog. A.P.F.: absolute pollen frequency. Profile of bog is shown by diagrammatic section at right of figure.

(Nymphæa and Castalia) near the surface may indicate a return to an open water stage of the bog caused by a relatively brief wet cycle.

Coon Lake Bog (8; Table 2, Fig. 3) is similar in its spectrum to the one described above. Dominance of Abies covers only at the lowest level, while Picea is dominant for a longer period. Both genera practically disappear from the diagram at the 3.8-meter level. A significant increase in the frequency of Ulmus to 8.5 percent appears at the same level. Pinus becomes the predominant pollen early in the history of the bog and continues in control throughout except for two short periods of Quercus dominance in the upper layers. A sharp decrease in Pinus and Quercus at the surface is probably due to the great increase in pollen of Compositæ (Table 2).

This bog is the only one investigated in which black spruce (*Picea mariana* BSP) occurs today, and this may account for the definite re-appearance of

TABLE 1. PERCENTAGES OF FOSSIL POLLEN FROM COON CREEK BOG

Depth in meters	Abies	Picea	Pinus	Alnus	Betula	Corylus	Carpinus	Carya	Acer	Quercus	Juglans	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.	Nymphæaceæ
.20	....	....	50.0	2.0	2.0	2.0	....	....	....	22.0	....	....	....	8.0	9.0	4.0	....
.40	....	1.0	24.0	....	8.0	6.0	....	....	....	36.0	....	2.0	4.0	6.0	10.0	3.0	....
.60	....	....	14.0	2.0	6.0	....	....	....	....	66.0	....	....	....	4.0	8.0	....	....
.80	....	....	20.0	10.0	15.0	....	....	....	....	32.0	....	2.0	....	8.0	12.0	3.0	....
1.00	....	2.0	40.0	1.0	4.0	....	....	....	....	30.0	....	....	....	6.0	11.0	4.0	....
1.20	....	....	50.0	5.0	3.0	....	....	....	....	17.0	....	....	....	6.0	13.0	....	7.0
1.40	....	....	60.0	....	6.0	....	....	....	....	25.0	....	....	....	3.0	5.0	2.0	....
1.60	....	....	33.0	2.0	6.0	....	....	....	....	40.0	....	....	....	4.0	12.0	2.0	1.0
1.80	....	....	25.0	5.0	3.0	....	....	....	....	43.0	....	....	....	9.0	10.0	5.0	....
2.00	....	....	5.0	....	3.0	3.0	....	....	....	60.0	....	....	2.0	8.0	13.0	6.0	....
2.20	....	....	18.0	2.0	10.0	2.0	....	....	....	30.0	....	....	2.0	14.0	20.0	2.0	....
2.40	....	....	50.0	5.0	5.0	....	....	....	....	20.0	....	....	....	10.0	10.0	....	....
2.60	1.0	....	60.0	....	....	2.0	....	....	....	20.0	....	....	2.0	3.0	6.0	4.0	2.0
2.80	....	....	52.0	....	1.0	....	....	....	....	23.0	....	....	1.0	8.0	11.0	2.0	2.0
3.00	....	....	61.0	....	....	....	....	....	....	19.0	....	....	....	2.0	11.0	5.0	2.0
3.20	....	....	44.0	1.0	1.0	....	....	....	....	24.0	....	....	2.0	10.0	10.0	5.0	3.0
3.40	2.0	3.0	49.0	....	1.0	....	....	....	....	22.0	....	....	....	6.0	9.0	8.0	....
3.60	....	2.0	48.0	....	2.0	....	....	....	....	28.0	....	....	....	4.0	6.0	10.0	....
3.80	....	6.0	54.0	....	2.0	....	....	....	....	25.0	....	1.0	....	8.0	3.0	3.0	....
4.00	....	4.0	30.0	....	1.0	....	....	....	....	30.0	....	....	2.0	16.0	11.0	6.0	....
4.20	....	3.0	33.0	....	1.0	1.0	....	....	....	39.0	....	....	....	9.0	10.0	4.0	....
4.40	....	....	22.0	....	6.0	....	....	....	....	27.0	....	....	7.0	11.0	23.0	4.0	....
4.60	1.5	1.0	40.0	1.0	1.5	0.5	....	....	....	18.0	1.0	....	12.0	7.0	15.0	2.0	....
4.80	....	....	50.0	1.0	1.5	....	....	0.5	....	15.0	....	1.0	12.5	4.0	11.0	3.0	0.5
5.00	....	2.0	52.0	1.0	4.5	....	1.0	....	1.5	8.0	....	1.0	8.5	4.0	14.0	1.0	0.5
5.20	....	1.5	89.0	0.5	1.0	1.5	....	....	....	4.0	....	....	2.0	0.5	....	....	....
5.40	....	1.0	83.5	0.5	3.5	0.5	....	....	....	4.5	....	....	2.5	1.5	1.0	0.5	1.0
5.60	....	12.0	87.5	....	3.5	....	....	....	....	2.0	....	....	0.5	0.5	....	....	....
5.80	3.0	19.0	66.0	....	4.5	1.0	....	....	....	1.0	....	....	4.5	0.5	0.5	....	....
6.00	6.0	22.5	50.0	0.5	6.0	....	....	....	....	10.0	....	....	3.0	0.5	1.5	....	....
6.20	17.5	61.5	8.5	....	3.0	....	....	....	0.5	4.0	....	....	1.0	1.5	4.5	....	0.5
6.40	23.0	48.0	8.5	....	6.5	0.5	....	....	....	6.5	....	....	....	3.5	3.0	0.5	....
6.60	28.0	54.0	10.5	....	0.5	....	....	....	....	2.0	....	....	1.0	2.5	1.5	....	....
6.80	75.0	23.5	0.5	....	....	....	....	....	....	1.0	....	....	....	....	....	....	....
7.00	89.0	9.0	0.5	....	....	....	....	....	....	....	....	....	....	1.0	0.5	....	....

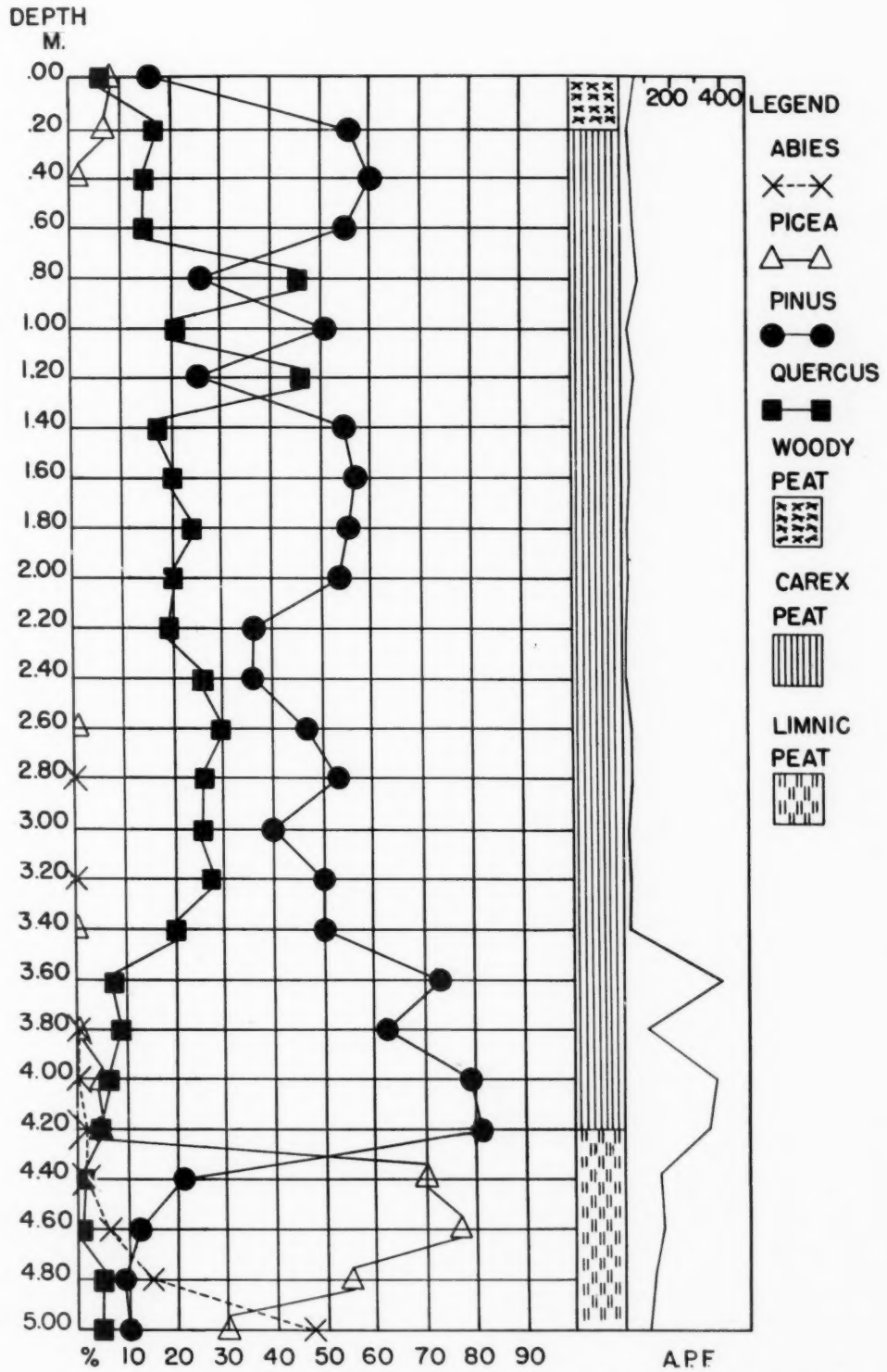

FIG. 3. Pollen diagram of Coon Lake bog. A.P.F.: absolute pollen frequency.

Picea pollen near the surface. Wilson and Galloway (1937) believe that an increase in spruce pollen near the surface of the Forestry Bog in Northern Wisconsin may be correlated with the appearance of the black spruce on the organic soils of the bog. It must be noted, however, that in several bogs of the present study where today no spruce occurs, its pollen also reappears at the upper levels, though less definitely than in the Coon Lake bog. So slight an increase of Picea seems hardly sufficient evidence to justify Fuller's assumption, in discussing profiles from the Lake Michigan region (1935), that such facts indicate a return to a cooler climate.

Linwood bog (4; Table 3, Fig. 4) also shows a profile similar to that of the Coon Creek deposit, Abies and Picea disappearing from the diagram very early in its development. The curve of Pinus quickly reaches its maximum of 82 percent at 5.4 meters and then rapidly declines. Quercus dominates from the 4.8 to the 4-meter level, but this is followed by a very marked fluctuation between Pinus and Quercus throughout the greater part of the diagram. Ulmus was sufficiently abundant in the region to record a frequency of 10 percent. at the 5-meter level.

Karmel bog (11; Table 4, Fig. 5). The record in this spectrum begins at the 4-meter level since the lowest four samples of marl failed to disclose the

TABLE 2. PERCENTAGES OF FOSSIL POLLEN FROM COON LAKE BOG

Depth in meters	Abies	Picea	Pinus	Tsuga	Alnus	Betula	Corylus	Carpinus	Juglans	Acer	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.	Nymphæaceæ	Ericaceæ
Surf.	....	8.0	16.0	....	6.0	5.0	2.0	....	....	....	6.0	....	....	9.0	31 0	13.0	....	4.0
0.20	....	6.0	56.0	....	5.0	4.0	....	....	....	....	17.0	....	....	8.0	4.0	....	....	....
0.40	....	2.0	60.0	1.0	4.0	4.0	....	....	....	....	15.0	....	....	7.0	7.0	....	....	....
0.60	....	....	55.0	....	6.0	11.0	1.0	....	....	....	15.0	....	2.0	2.0	8.0	....	....	....
0.80	....	....	27.0	....	1.0	5.0	2.0	....	1.0	....	45.0	....	2.0	6.0	9.0	2.0	....	....
1.00	....	....	51.0	....	4.0	4.0	....	1.0	....	....	21.0	1.0	....	4.0	14.0	....	....	....
1.20	....	....	27.0	....	3.0	9.0	1.0	....	....	....	47.0	....	2.0	5.0	6.0	....	....	....
1.40	....	....	55.0	....	2.0	4.0	2.0	....	....	....	17.0	....	....	4.0	12.0	4.0	....	....
1.60	....	....	58.0	....	2.0	....	....	....	....	....	20.0	....	1.0	6.0	11.0	2.0	....	....
1.80	....	1.0	56.0	....	....	1.0	....	....	....	....	23.0	....	....	6.0	10.0	3.0	....	....
2.00	....	....	53.0	....	2.0	3.0	....	....	....	....	10.0	....	....	12.0	16.0	4.0	....	....
2.20	....	....	37.0	....	....	2.0	....	....	....	....	19.0	....	....	16.0	16.0	10.0	....	....
2.40	....	....	36.0	....	1.0	3.0	1.0	....	....	....	26.0	....	....	11.0	12.0	10.0	....	....
2.60	....	1.5	47.5	....	2.5	5.5	0.5	....	....	....	30.0	....	1.0	3.0	6.0	2.0	0.5	....
2.80	0.5	....	52.5	....	....	1.5	0.5	....	0.5	....	27.5	....	....	2.5	12.5	1.5	0.5	....
3.00	....	....	40.0	....	....	1.5	....	....	1.0	1.0	26.5	0.5	2.0	4.5	15.5	7.0	....	....
3.20	0.5	....	50.0	....	....	2.5	....	....	....	....	28.5	....	2.5	4.0	8.0	1.5	....	....
3.40	....	0.5	50.0	....	1.5	5.0	1.0	....	0.5	0.5	20.0	1.0	4.0	1.5	8.5	4.0	2.0	....
3.60	....	....	72.5	....	....	2.5	....	....	....	....	8.5	....	5.0	3.5	5.0	2.0	1.0	....
3.80	0.5	0.5	62.5	....	0.5	4.0	....	....	....	....	9.0	1.0	8.5	7.0	5.5	0.5	0.5	....
4.00	0.5	3.0	80.5	....	....	2.0	....	....	....	....	5.5	....	5.0	2.0	1.5	....	....	....
4.20	1.5	3.0	81.5	....	0.5	5.5	....	....	....	....	3.5	....	2.0	0.5	1.5	....	....	....
4.40	2.0	70.0	21.0	....	....	2.5	....	....	....	....	1.5	....	1.0	0.5	1.5	....	....	....
4.60	5.0	77.5	11.0	....	....	2.5	....	....	....	....	1.0	....	0.5	1.0	1.0	....	0.5	....
4.80	15.5	55.0	8.5	....	....	5.0	....	....	....	....	4.5	....	1.0	0.5	4.5	0.5	....	....
5.00	47.5	31.0	10.0	....	....	2.0	....	....	....	....	4.5	....	..	1.0	4.0	....	....	....

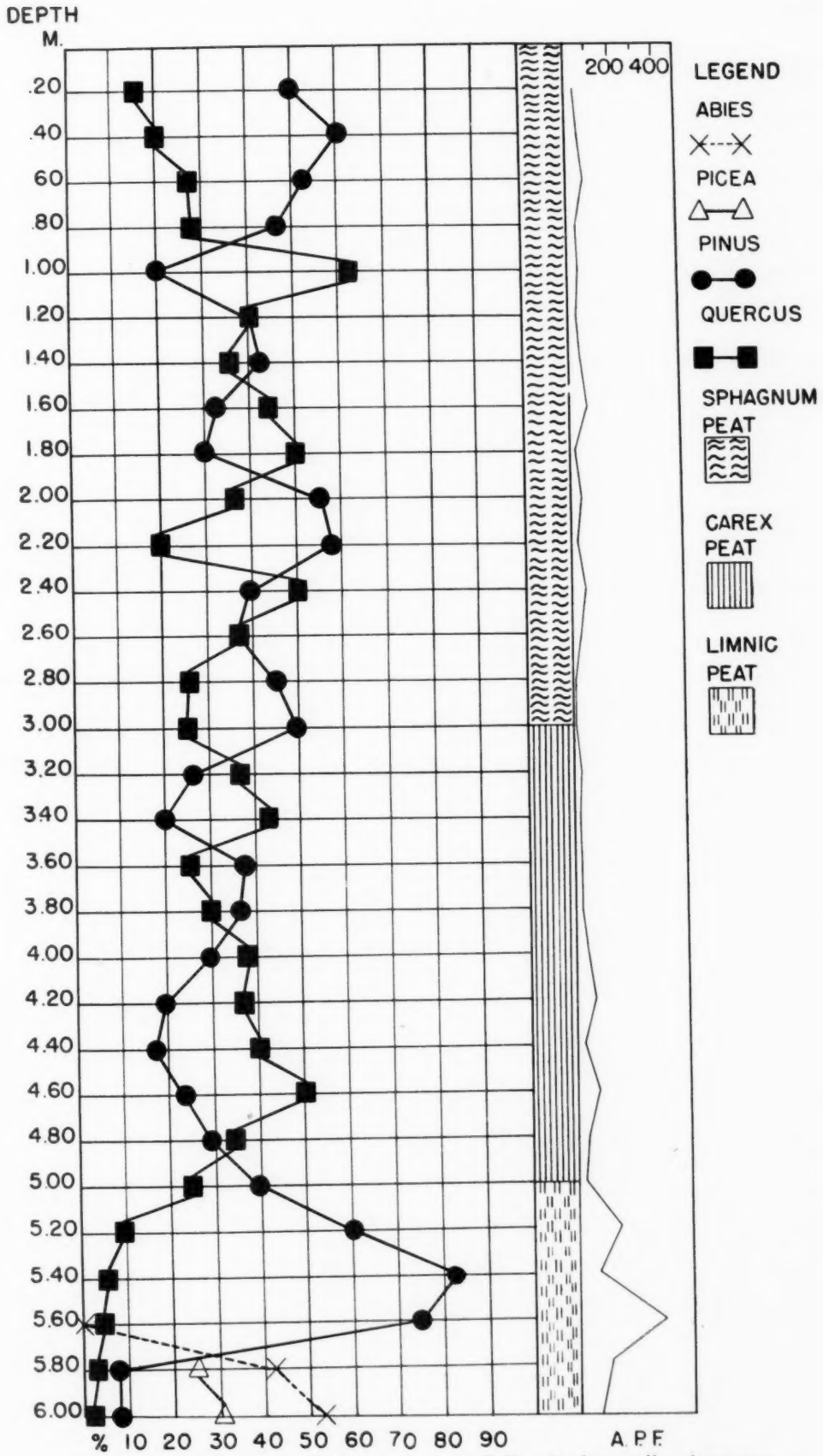

FIG. 4. Pollen diagram of Linwood bog. A.P.F.: absolute pollen frequency.

presence of fossils. Its pollen curves are similar to those of the type. Abies and Picea, respectively, reach a maximum and then decline; the former is eliminated at 3.4 meters while Picea continues to appear here and there in minor amount upward. Pinus rises to dominance at 3.4 meters but quickly gives way to a Quercus maximum extending from the 3.2 to the 2.6-meter level. After a period of fluctuating dominance, Pinus again gains control at 1.8 meters and maintains it to the surface. The sharp decrease in the frequency of both genera in the surface peat is probably due to the great increase in pollen of Compositæ, which comprises 30 percent of the total count.

Princeton bog (12; Table 5, Fig. 6). This section is but 3.4 meters in depth, yet it carries a complete record of the microfossil succession. Following the initial dominance of Abies and Picea, respectively, a striking increase in Abies pollen to a frequency of 76 percent occurs at 2.8 meters. Picea again supersedes Abies and reaches a frequency of 35 percent, then disappears abruptly from the lower two-thirds of the spectrum. Initial dominance of Pinus occurs at the 2.6-meter level. As in the Karmel bog, an abrupt de-

TABLE 3. PERCENTAGES OF FOSSIL POLLEN FROM LINWOOD BOG

Depth in meters	Abies	Picea	Pinus	Alnus	Betula	Carpinus	Corylus	Juglans	Salix	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.	Nymphæaceæ
0.20	....	....	50.0	3.0	9.0	....	....	....	....	15.0	....	4.0	2.0	17.0	....	....
0.40	....	....	61.0	1.0	9.0	....	....	....	....	20.0	....	1.0	3.0	5.0	....	....
0.60	....	....	52.0	....	13.0	....	....	....	....	27.0	....	....	3.0	5.0	....	....
0.80	....	....	47.0	2.0	6.0	....	1.0	....	....	28.0	1.0	....	7.0	8.0	....	....
1.00	....	....	20.0	....	2.0	....	....	....	....	62.0	....	2.0	6.0	7.0	1.0	....
1.20	....	....	41.0	....	6.0	....	1.0	....	....	40.0	....	1.0	6.0	2.0	3.0	....
1.40	....	....	42.0	1.0	7.0	....	....	....	....	36.0	2.0	3.0	6.0	3.0	....	....
1.60	....	....	32.0	1.0	7.0	....	....	....	....	45.0	....	1.0	10.0	4.0	....	....
1.80	....	....	30.0	....	5.0	....	....	....	....	50.0	....	4.0	6.0	2.0	3.0	....
2.00	....	....	56.0	1.0	2.0	....	....	....	....	37.0	....	....	2.0	1.0	1.0	....
2.20	....	....	58.0	....	3.0	1.0	....	....	....	19.0	....	1.0	5.0	12.0	1.0	....
2.40	....	....	39.0	1.0	1.0	....	....	....	....	50.0	....	....	6.0	2.0	1.0	....
2.60	....	....	37.0	1.0	4.0	....	....	1.0	....	36.0	....	....	9.0	12.0	2.0	....
2.80	....	....	45.0	1.0	4.0	....	1.0	....	....	27.0	....	1.0	10.0	12.0	....	....
3.00	....	....	49.0	2.0	2.0	....	....	....	....	26.0	....	....	9.0	13.0	1.0	....
3.20	....	....	27.0	1.0	....	....	....	....	....	37.0	....	....	12.0	22.0	1.0	....
3.40	....	....	20.0	1.0	1.0	....	....	....	....	43.0	....	....	15.0	17.0	2.0	....
3.60	....	....	38.0	....	3.0	....	....	....	....	26.0	2.0	1.0	12.0	17.0	2.0	....
3.80	....	....	37.0	....	4.0	....	....	....	....	30.0	....	....	17.0	10.0	3.0	....
4.00	....	....	29.0	....	2.0	....	....	....	....	38.0	1.0	2.0	13.0	11.0	4.0	....
4.20	....	....	19.0	....	1.0	....	....	....	....	37.0	....	4.0	18.0	15.0	6.0	....
4.40	....	....	18.0	2.0	2.0	0.5	....	....	....	40.5	0.5	4.0	10.5	22.0	2.5	....
4.60	....	....	23.0	....	2.0	....	....	....	1.0	50.0	1.0	....	9.0	11.0	3.0	....
4.80	....	....	29.0	....	2.5	....	0.5	....	....	34.0	....	5.5	11.5	12.5	4.0	....
5.00	....	....	39.0	....	9.0	0.5	1.5	....	....	25.0	....	10.0	3.5	13.0	1.5	....
5.20	....	....	60.0	0.5	4.0	0.5	2.5	....	....	9.5	1.0	7.5	5.0	7.0	1.0	1.5
5.40	....	....	82.0	....	2.5	....	....	....	....	6.5	1.0	3.0	2.5	1.0	1.5	....
5.60	0.5	....	76.5	2.0	4.0	1.0	1.0	0.5	....	4.5	....	5.5	2.0	2.0	1.0	....
5.80	42.0	25.5	8.5	1.0	8.5	....	1.5	....	....	3.0	0.5	....	5.0	2.0	....	2.0
6.00	53.0	31.0	8.5	....	1.0	....	....	....	....	1.0	....	1.0	3.0	3.0	....	....

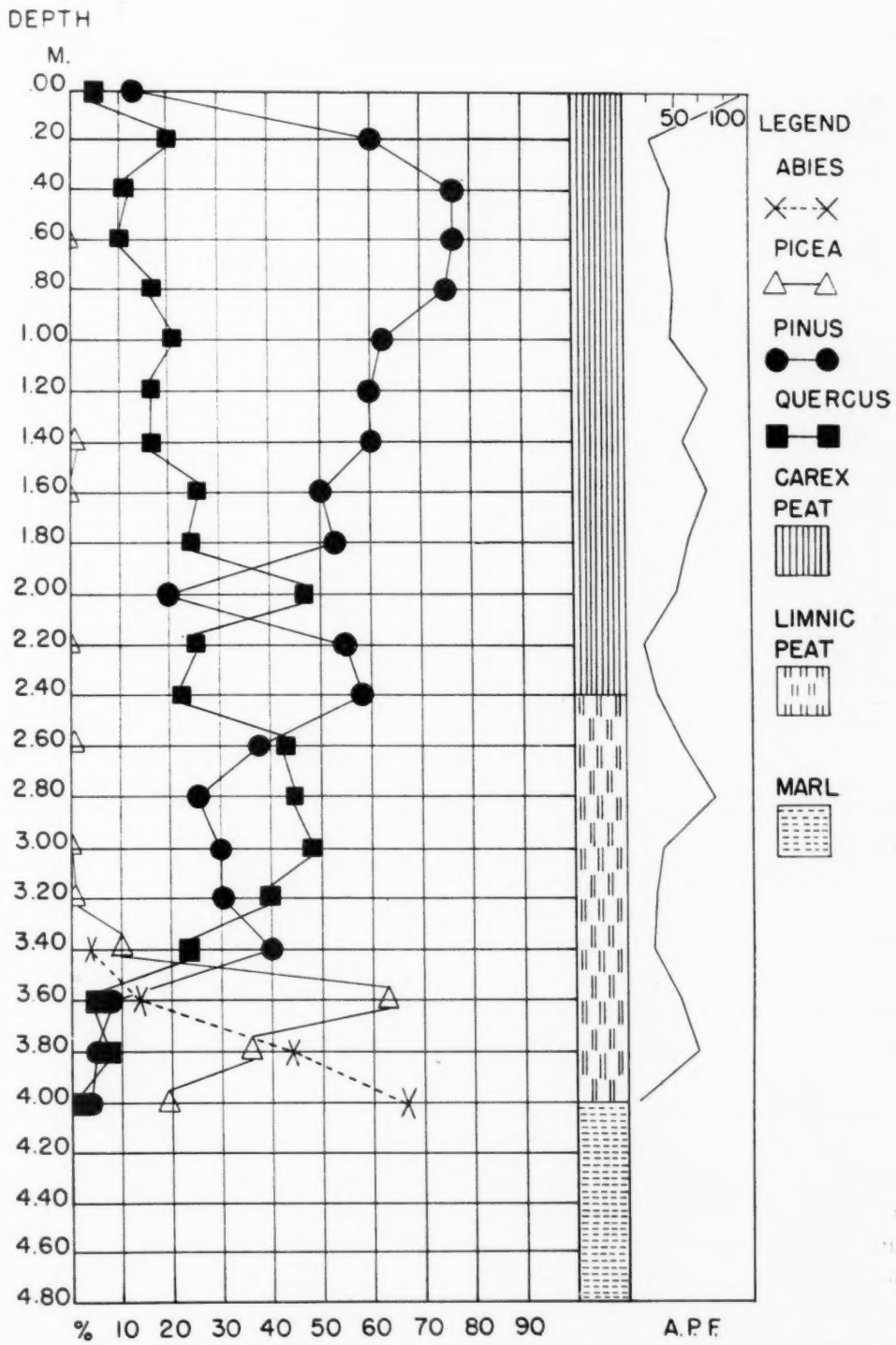

FIG. 5. Pollen diagram of Karmel bog. A.P.F.: absolute pollen frequency.

TABLE 4. PERCENTAGES OF FOSSIL POLLEN FROM KARMEL BOG

Depth in meters	Abies	Picea	Pinus	Alnus	Betula	Carpinus	Corylus	Acer	Juglans	Populus	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.	Nymphæaceæ
Surf.	....	....	12.0	8.0	21.0	....	8.0	....	....	....	4.0	....	....	10.0	30.0	7.0	....
0.20	....	....	60.0	1.5	10.0	....	....	....	....	....	20.0	3.5	....	0.5	3.5	1.0	....
0.40	....	....	76.5	2.0	3.5	....	....	....	....	....	11.5	0.5	....	3.0	3.0	....	....
0.60	....	0.5	76.5	2.0	5.0	....	....	....	....	....	10.0	....	....	4.0	2.0	....	....
0.80	....	....	75.0	....	1.5	....	0.5	....	....	....	17.0	....	....	3.5	1.0	....	....
1.00	....	....	62.5	2.0	4.5	....	....	....	0.5	....	21.0	0.5	1.0	5.5	2.0	....	0.5
1.20	1.0	....	59.5	3.0	10.5	....	....	....	0.5	....	17.0	....	1.5	4.5	2.0	0.5	....
1.40	....	1.5	60.0	2.0	5.5	1.0	....	....	2.0	....	18.0	1.0	2.5	2.5	3.0	....	1.0
1.60	....	0.5	49.5	1.0	4.0	....	....	....	....	....	27.0	2.0	3.5	9.0	3.0	0.5	....
1.80	....	....	53.5	....	9.0	....	....	....	....	....	24.5	0.5	....	8.5	1.5	....	1.5
2.00	....	....	19.5	0.5	3.5	....	....	....	....	....	47.5	0.5	....	18.5	9.0	1.0	....
2.20	....	0.5	54.5	....	2.5	....	1.0	....	....	2.0	25.5	....	....	7.5	5.0	4.5	....
2.40	....	....	58.5	....	3.0	....	....	0.5	....	2.0	22.0	1.0	2.0	5.5	3.0	2.0	0.5
2.60	....	1.5	38.0	0.5	1.5	....	....	....	....	....	43.5	....	....	4.5	5.0	5.5	....
2.80	....	....	27.0	....	2.5	....	....	....	....	....	45.0	....	0.5	8.5	7.5	10.0	....
3.00	....	0.5	29.5	....	0.5	....	....	....	....	....	48.0	....	0.5	7.5	4.5	9.0	....
3.20	....	1.5	30.5	....	3.0	....	....	....	....	....	39.0	....	....	10.0	7.0	7.5	....
3.40	4.5	10.5	40.0	....	0.5	....	....	....	....	....	23.0	0.5	....	5.5	8.5	8.0	....
3.60	13.5	63.0	8.0	0.5	7.0	....	....	....	....	....	4.5	....	....	1.0	2.5	....	....
3.80	44.0	35.5	5.0	....	1.0	....	....	....	....	....	8.0	1.0	....	1.0	5.5	....	....
4.00	67.5	19.5	3.5	....	....	....	....	....	....	....	3.0	....	....	4.5	2.0	....	....
4.20	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
4.40	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
4.60	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
4.80	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....

crease in the frequency of Pinus at the surface may be due to the greater relative abundance of Compositæ pollen.

Ham Lake bog (10; Table 6, Fig. 7) may be considered most typical of five bogs in which Picea is the first dominant pollen at the bottom, while Abies is present in but minor amount. The spectrum begins with a definite maximum of Picea showing a frequency of 86.5 percent. Abies, Pinus and Quercus each show less than 5 percent at the same level. As Picea rapidly declines, Pinus reaches its initial maximum at 4.6 meters, and except for two brief periods of Quercus dominance in the middle part of the profile continues in control to the surface.

Elk River bog (13; Table 7, Fig. 8) shows a pollen spectrum very similar to that of the Ham Lake deposit. A high frequency of Picea pollen, 79.5 percent, is recorded in the bottom peat, while Abies is present only in minor amount. This profile differs from those described above in that the curves of Pinus and Quercus show no fluctuation throughout the spectrum. Pinus continues up one side of the diagram and Quercus up the other. This is the reverse of the relative positions of these two genera in the Illinois bogs (Voss, 1934), where a long period of Quercus dominance follows the decline of Abies and Picea. Due to the very low pollen frequency of the peat (less

than 1 per square centimeter) a break occurs in the record from the 3-meter to the 1.8-meter level.

Rice Lake bog (7; Table 8, Fig. 9). The section here is not as deep as the last but its pollen curves are in general quite similar. Picea pollen is dominant for an extended period in the lower levels and is superseded by Pinus, which remains in control throughout the remainder of the section. No Quercus maximum is recorded in this profile.

Cedar Creek bog (1; Table 9, Fig. 10) shows the deepest section of peat and marl encountered in the present study. At a depth of 11 meters the sampler was still in the highly compacted non-shell marl. Repeated efforts to penetrate deeper resulted in damage to the instrument. The lowest samples obtained indicate that the bottom was not far distant. The pollen curves

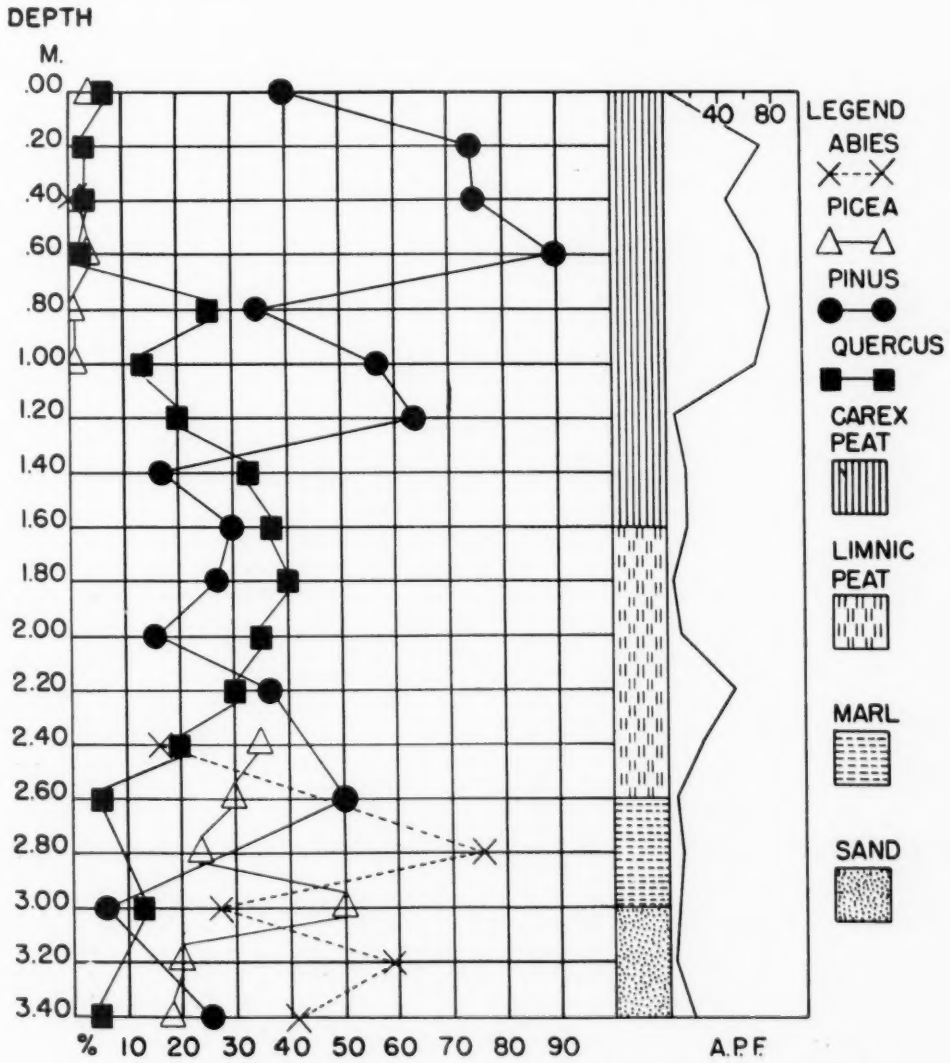

FIG. 6. Pollen diagram of Princeton bog. A.P.F.: absolute pollen frequency.

TABLE 5. PERCENTAGES OF FOSSIL POLLEN FROM HAM LAKE BOG

Depth in meters	Abies	Picea	Pinus	Thuja	Alnus	Betula	Carpinus	Corylus	Juglans	Salix	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.	Nymphaeaceæ
0.20	....	....	86.0	....	0.5	0.5	....	....	....	....	4.0	1.0	....	2.0	3.5	2.5	....
0.40	....	....	85.0	....	0.5	2.0	....	....	....	0.5	3.0	0.5	0.5	4.5	3.5	....	....
0.60	....	....	78.0	....	....	1.0	....	....	....	....	9.0	0.5	2.5	5.5	1.5	2.0	....
0.80	....	....	71.0	....	1.0	3.5	....	....	....	....	19.5	....	1.0	2.5	1.5	0.5	....
1.00	....	....	62.5	....	1.5	7.5	....	....	....	....	16.5	0.5	1.5	2.5	4.5	3.0	....
1.20	....	....	72.0	....	0.5	1.5	....	0.5	1.0	....	12.0	....	0.5	3.0	5.0	....	4.0
1.40	....	....	57.5	....	....	4.0	....	1.5	....	....	17.5	0.5	0.5	4.0	7.5	1.0	4.0
1.60	....	....	58.0	....	1.5	2.5	....	....	....	....	22.0	0.5	2.5	7.0	6.0	....	0.5
1.80	....	....	59.0	0.5	0.5	2.5	....	....	1.0	....	27.5	0.5	1.5	5.0	....	2.0	1.0
2.00	....	....	54.0	0.5	0.5	4.0	....	1.0	....	0.5	28.0	....	1.5	5.0	2.5	2.5	2.5
2.20	....	....	6.0	....	3.5	4.5	....	1.0	0.5	....	60.0	....	2.5	8.5	11.0	2.5	....
2.40	....	....	15.5	....	0.5	6.5	....	....	....	....	52.0	0.5	2.0	4.5	12.5	3.0	....
2.60	....	....	48.0	....	....	1.0	0.5	....	....	....	33.0	1.0	1.5	1.5	9.5	4.0	....
2.80	....	....	50.0	....	....	2.5	0.5	....	....	1.5	27.5	....	1.5	8.0	5.5	3.0	....
3.00	....	....	6.0	....	0.5	4.0	....	....	....	....	63.0	....	4.0	8.5	11.0	5.0	....
3.20	....	....	1.0	....	....	3.5	....	....	....	....	62.5	....	6.0	12.0	13.5	1.5	....
3.40	....	....	17.0	....	....	4.0	....	....	....	....	41.5	0.5	9.0	12.0	14.0	2.0	....
3.60	....	....	17.0	....	....	4.0	....	....	....	....	40.5	....	4.0	32.0	25.0	6.0	....
3.80	....	1.0	46.0	....	0.5	4.5	....	0.5	....	....	21.5	0.5	10.0	5.5	6.0	4.0	....
4.00	....	1.0	75.0	....	0.5	6.0	....	....	....	....	8.5	....	5.0	2.0	1.0	1.0	....
4.20	0.5	1.0	75.0	....	....	1.5	....	....	....	....	7.0	....	....	3.0	2.0	1.0	....
4.40	....	5.0	73.0	....	0.5	9.0	....	....	....	....	7.5	....	1.5	1.0	2.0	0.5	....
4.60	2.0	26.0	53.0	....	0.5	9.5	....	....	....	....	3.5	....	2.5	2.5	3.0	....	....
4.80	5.0	71.0	5.5	....	0.5	8.5	....	....	....	....	7.5	....	....	....	1.5	0.5	....
5.00	2.5	70.0	6.0	....	....	4.5	....	....	....	....	9.5	....	....	5.5	1.0	0.5	....
5.20	4.5	86.5	1.0	....	....	....	....	....	....	....	1.5	....	....	1.5	1.0	....	....

TABLE 6. PERCENTAGES OF FOSSIL POLLEN FROM PRINCETON BOG

Depth in meters	Abies	Picea	Pirus	Alnus	Betula	Corylus	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.
Surf.	...	3.0	39.0	6.0	...	...	6.0	2.0	...	12.0	32.0	...
0.20	...	2.0	73.0	...	...	...	2.0	...	...	15.0	4.0	4.0
0.40	1.0	2.0	75.0	...	1.0	1.0	2.0	...	...	14.0	4.0	...
0.60	...	3.0	89.0	...	2.0	...	2.0	...	...	4.0	...	...
0.80	...	1.0	34.0	3.0	1.0	...	26.0	2.0	...	13.0	16.0	4.0
1.00	...	1.0	58.0	2.0	1.0	...	13.0	...	...	15.0	10.0	...
1.20	...	...	62.0	...	...	...	20.0	...	...	18.0	...	...
1.40	...	2.0	18.0	10.0	2.0	2.0	32.0	...	...	22.0	10.0	2.0
1.60	...	...	30.0	4.0	10.0	...	38.0	...	4.0	4.0	...	...
1.80	...	...	28.0	2.0	2.0	...	40.0	...	...	20.0	8.0	...
2.00	...	...	16.0	4.0	4.0	...	36.0	...	...	24.0	...	...
2.20	...	...	37.0	...	7.0	...	30.0	...	...	14.0	7.0	5.0
2.40	18.0	35.0	...	...	...	...	20.0	...	...	15.0	10.0	...
2.60	....	30.0	50.0	...	...	...	4.0	...	...	...	6.0	10.0
2.80	76.0	24.0	...	...	...	...	...	...	...	...	...	...
3.00	27.0	49.0	6.0	...	...	...	12.0	...	...	6.0	...	...
3.20	58.0	20.0	...	...	...	...	...	...	...	17.0	...	5.0
3.40	42.0	18.0	26.0	2.0	2.0	...	4.0	...	...	6.0	...	...

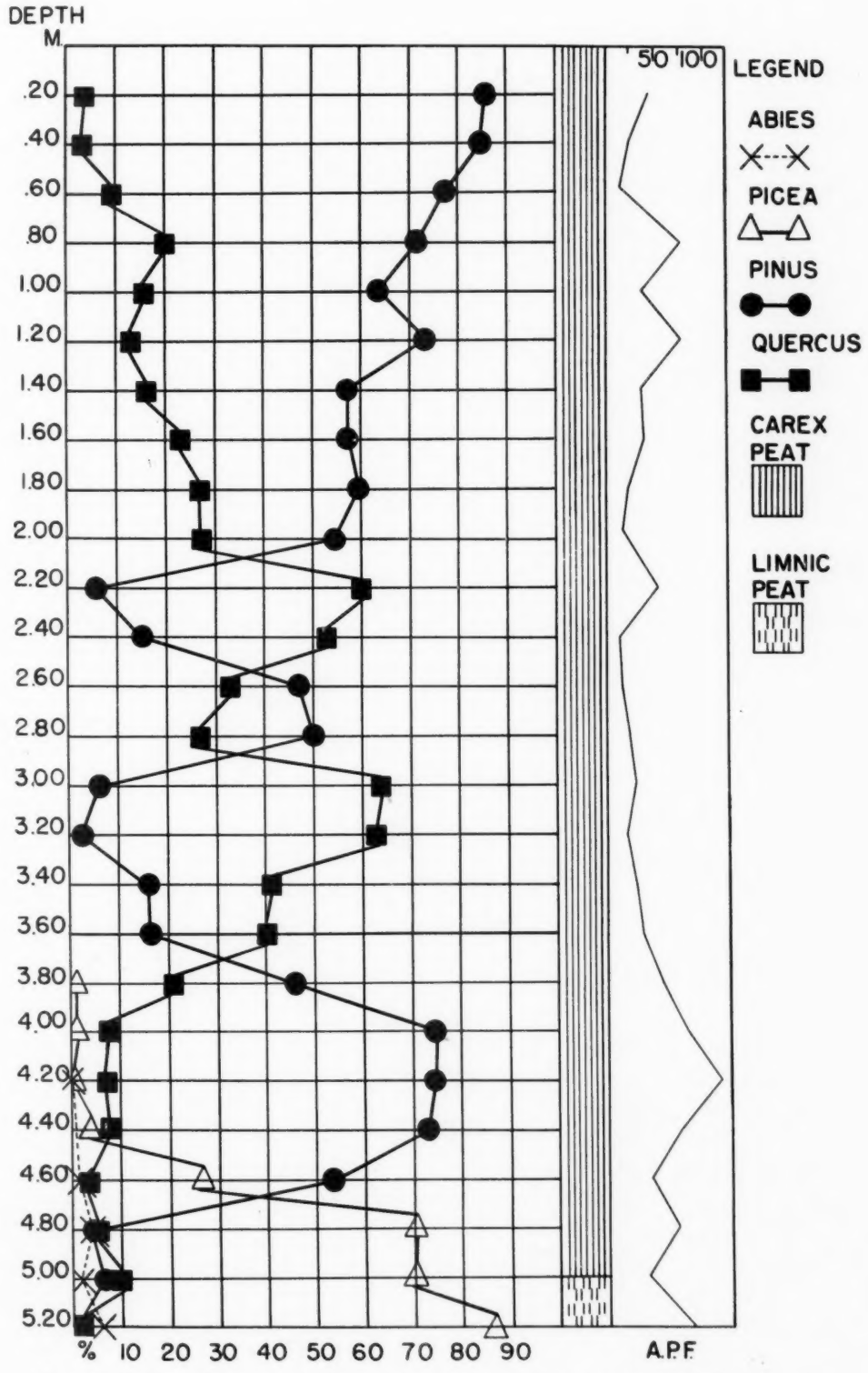

FIG. 7. Pollen diagram of Ham Lake bog. A.P.F.: absolute pollen frequency.

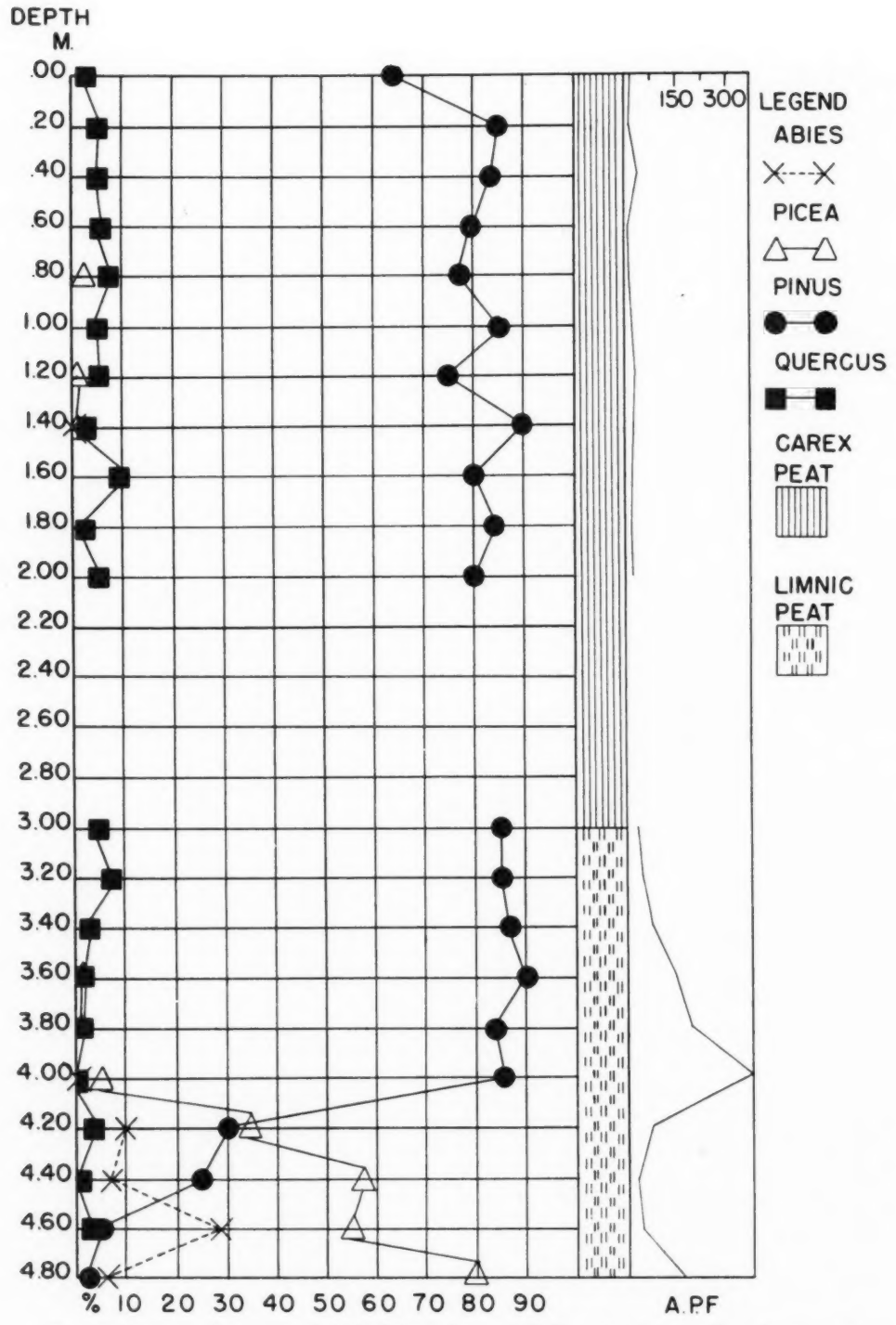

FIG. 8. Pollen diagram of Elk River bog. A.P.F.: absolute pollen frequency.

TABLE 7. PERCENTAGES OF FOSSIL FROM ELK RIVER BOG

Depth in meters	Abies	Picea	Pinus	Alnus	Betula	Corylus	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.	Nymphæaceæ
Surf.	....	....	64.0	....	....	....	2.0	1.0	....	14.0	15.0	4.0	....
0.20	....	....	84.0	....	....	....	4.0	....	....	8.0	4.0	....	....
0.40	....	....	83.0	....	....	....	5.0	1.0	....	7.0	4.0	....	....
0.60	....	....	79.0	....	1.0	....	5.0	....	....	2.0	9.0	1.0	....
0.80	....	2.0	78.0	....	....	....	8.0	....	....	3.0	6.0	3.0	....
1.00	....	....	84.0	....	3.0	....	....	....	....	5.0	3.0	2.0	....
1.20	....	1.0	75.0	....	1.0	....	5.0	2.0	....	6.0	8.0	2.0	....
1.40	1.0	1.0	89.0	....	....	....	....	....	....	4.0	3.0	....	....
1.60	....	....	80.0	....	2.0	....	9.0	....	....	6.0	2.0	1.0	....
1.80	....	....	84.0	....	....	2.0	2.0	....	....	8.0	4.0	4.0	....
2.00	....	....	80.0	....	....	....	4.0	....	....	4.0	12.0	....	....
2.20	....	....	....	....	....	....	....	....	....	....	....	....	....
2.40	....	....	....	....	....	....	....	....	....	....	....	....	....
2.60	....	....	....	....	....	....	....	....	....	....	....	....	....
2.80	....	....	....	....	....	....	....	....	....	....	....	....	....
3.00	....	....	85.0	....	....	....	4.0	....	....	7.0	3.0	1.0	....
3.20	....	....	86.0	2.0	2.0	....	8.0	....	....	2.0	....	....	....
3.40	....	....	88.5	....	5.0	....	2.0	....	3.0	1.5	....	....	....
3.60	....	1.5	90.5	....	1.0	....	1.5	....	3.0	1.0	0.5	....	1.0
3.80	....	1.0	83.0	....	4.5	....	1.5	....	3.5	4.0	1.0	....	1.5
4.00	1.5	4.5	85.0	....	2.0	....	1.0	....	2.0	2.5	0.5	....	1.0
4.20	10.0	35.0	31.5	....	8.0	....	3.5	....	2.0	4.0	2.0	....	4.0
4.40	7.5	57.5	24.0	....	1.5	....	1.0	....	0.5	5.0	....	....	2.5
4.60	28.5	55.5	4.5	0.5	1.0	....	2.0	....	0.5	4.0	1.5	0.5	2.0
4.80	6.5	79.5	4.5	....	3.0	....	....	....	....	4.0	2.0	....	0.5

TABLE 8. PERCENTAGES OF FOSSIL POLLEN FROM RICE LAKE BOG

Depth in meters	Abies	Picea	Pinus	Alnus	Betula	Corylus	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.	Nymphaeaceæ
0.20	....	....	70.0	....	3.0	3.0	17.0	....	....	2.0	5.0	....	....
0.40	....	....	55.0	....	4.0	3.0	25.0	....	....	6.0	7.0	....	....
0.60	....	....	47.0	....	6.0	....	36.0	....	....	5.0	4.0	2.0	....
0.80	....	1.0	55.0	....	3.0	....	32.0	....	....	2.0	7.0	....	....
1.00	....	....	60.0	....	2.0	....	20.0	....	....	8.0	7.0	3.0	....
1.20	....	1.0	65.0	....	....	....	17.0	3.0	....	7.0	3.0	4.0	....
1.40	....	....	48.0	1.0	1.0	....	34.0	....	....	7.0	7.0	2.0	....
1.60	....	1.0	57.0	2.0	1.0	1.0	27.0	....	....	4.0	5.0	2.0	....
1.80	....	2.0	58.0	2.0	....	....	18.0	....	....	2.0	12.0	6.0	....
2.00	....	2.0	50.0	1.0	3.0	....	25.0	1.0	....	7.0	10.0	1.0	....
2.20	....	....	80.0	....	....	....	12.0	....	....	1.0	5.0	2.0	....
2.40	....	....	96.0	....	1.0	....	2.0	....	....	....	1.0	....	....
2.60	....	....	80.0	....	3.0	....	5.0	....	4.0	3.0	5.0	....	....
2.80	....	2.0	95.0	....	....	....	3.0	....	....	....	....	....	....
3.00	....	1.0	94.0	....	....	....	3.0	....	....	1.0	1.0	....	....
3.20	....	1.0	87.0	....	5.0	1.0	4.0	....	....	2.0	....	....	....
3.40	2.0	25.0	68.0	....	....	....	2.0	....	....	....	2.0	....	1.0
3.60	5.0	52.0	33.0	....	2.0	....	4.0	....	....	2.0	2.0	....	....
3.80	8.0	78.0	3.0	....	....	....	4.0	....	....	3.0	1.0	2.0	1.0
4.00	9.0	62.0	20.0	....	2.0	....	3.0	....	1.0	1.0	2.0	....	....
4.20	17.0	67.0	4.0	....	....	1.0	5.0	....	....	1.0	3.0	2.0	....
4.40	30.0	63.0	....	....	....	....	5.0	....	....	....	2.0	....	....

are similar to those of Rice Lake bog except in the case of Abies. In the lowest level its frequency is very low, but at 10 meters it increases to a maximum of 45 percent, then disappears very abruptly from the diagram. Samples taken at closer intervals might have disclosed the same gradual decline of Abies that has been noted in all the preceding spectra. It is prob-

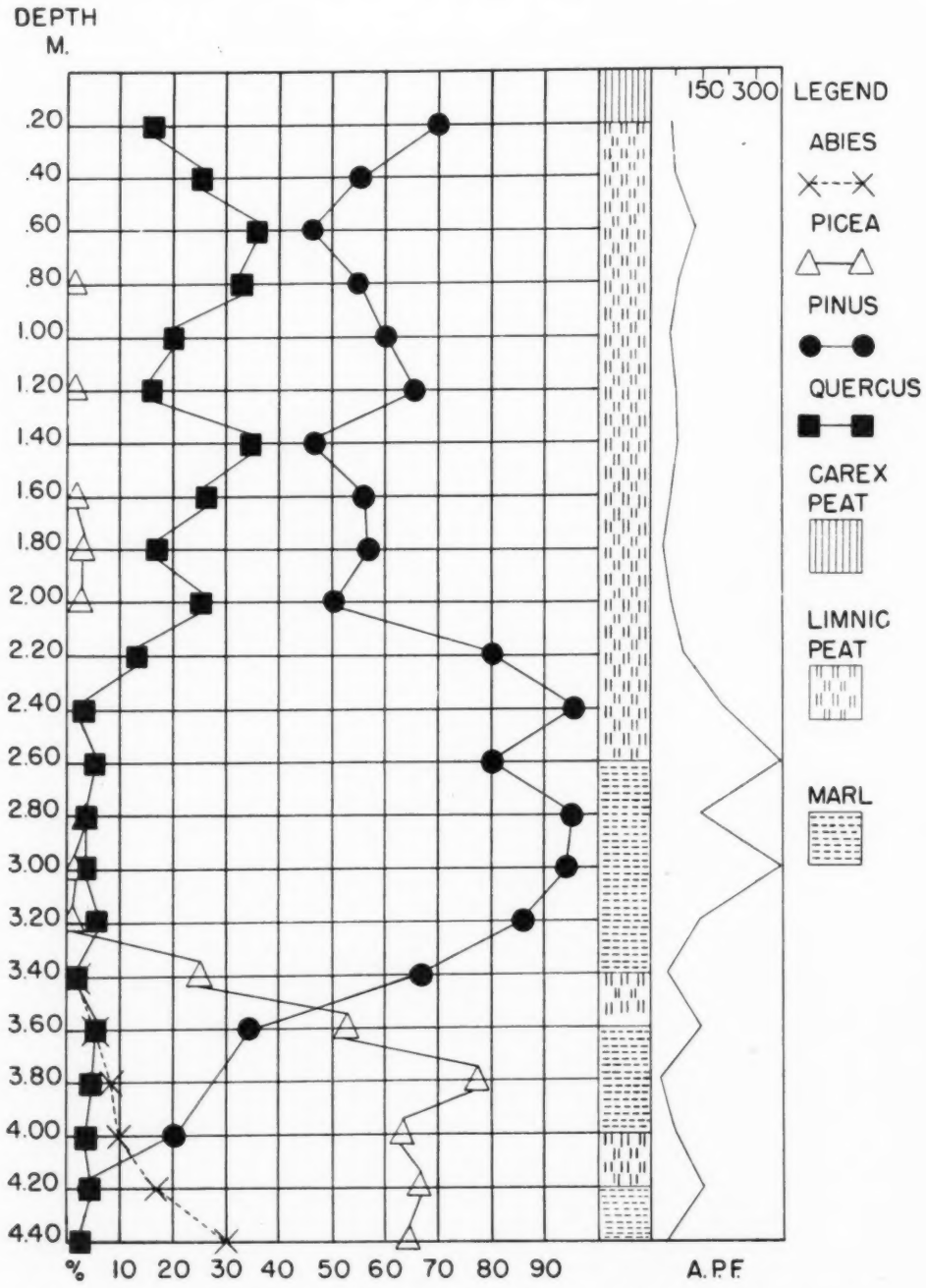

FIG. 9. Pollen diagram of Rice Lake bog. A.P.F.: absolute pollen frequency.

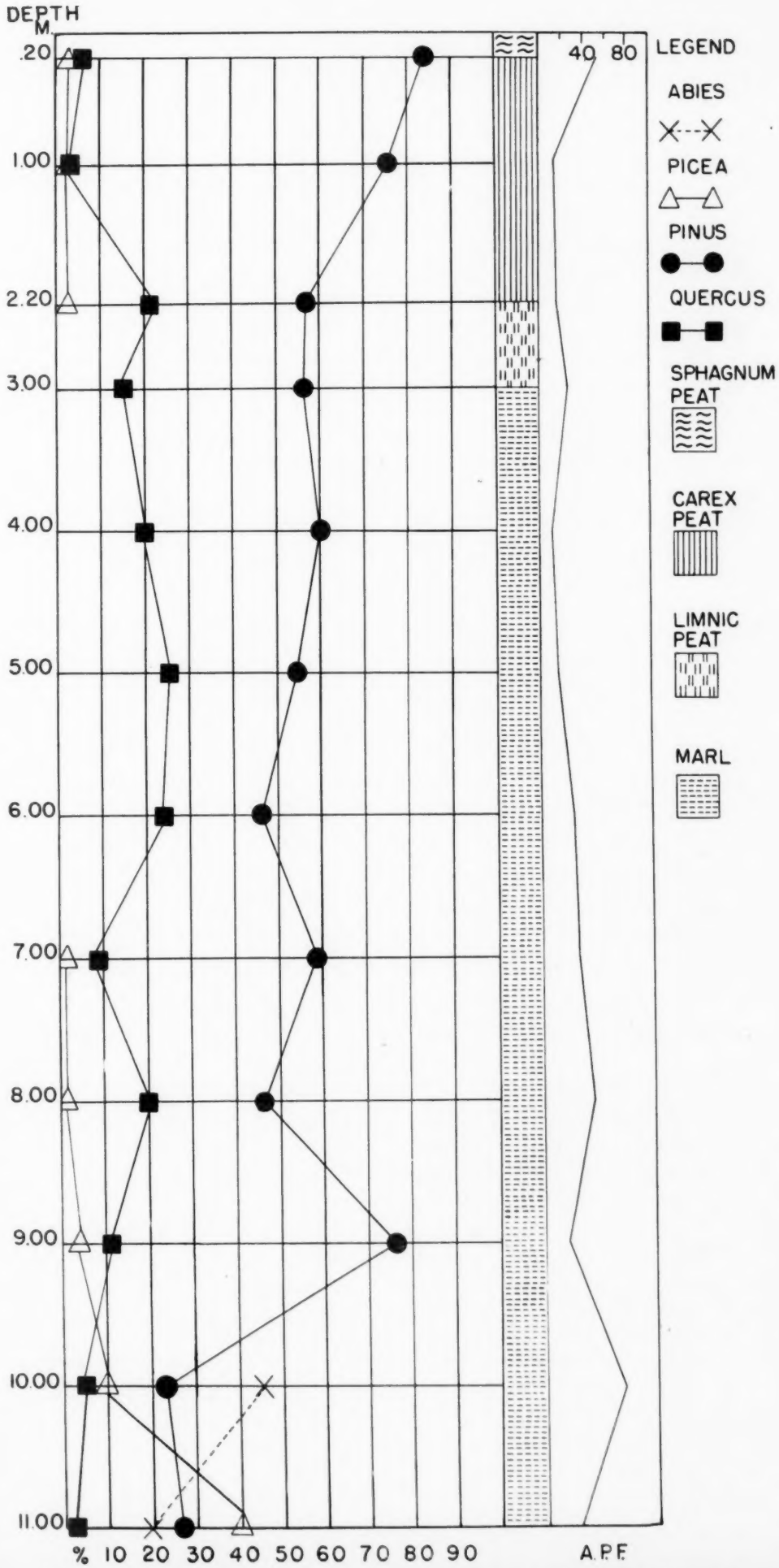

FIG. 10. Pollen diagram of Cedar Creek bog. A.P.F.: absolute pollen frequency.

able that this Abies maximum is a second return to dominance as in the Princeton profile (Fig. 6) while the record of the first may be present in the lower sediments which were not obtained. Quercus and Pinus pollen is present at all levels in the spectrum but their curves remain widely separated, with Pinus dominant throughout. A very slight increase in Picea pollen appears in the upper layers although this tree is not present today in the immediate vicinity. Voss (1934) attributes a similar increase in spruce near the surface of two bogs in Wisconsin to the presence of the bog spruce *(P. mariana)* on the surrounding mature bogs. The same explanation seems tenable here, since *P. mariana* BSP has been found less than two miles away.

TABLE 9. PERCENTAGES OF FOSSIL POLLEN FROM CEDAR CREEK BOG

Depth in meters	Abies	Picea	Pinus	Alnus	Betula	Corylus	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.
0.20	....	3.0	83.0	...	...	...	6.0	...	1.0	5.0	1.0	1.0
1.00	....	2.0	76.0	...	4.0	2.0	4.0	...	2.0	10.0	...	...
2.40	....	2.0	58.0	3.0	2.0	...	21.0	1.0	...	10.0	3.0	...
3.00	....	...	56.0	1.0	1.0	3.0	15.0	11.0	...	4.0	8.0	1.0
4.00	....	...	60.0	1.0	2.0	1.0	20.0	2.0	...	5.0	4.0	5.0
5.00	....	...	53.0	...	...	...	26.0	2.0	1.0	6.0	6.0	6.0
6.00	....	...	46.0	...	1.0	1.0	23.0	1.0	...	10.0	15.0	3.0
7.00	....	1.0	59.0	...	...	2.0	9.0	...	1.0	9.0	14.0	5.0
8.00	....	1.0	47.0	...	2.0	...	20.0	...	2.0	12.0	12.0	4.0
9.00	....	4.0	78.0	...	...	...	11.0	...	2.0	1.0	1.0	3.0
10.00	45.0	10.0	22.0	...	18.0	...	5.0	...	...	...	...	...
11.00	19.0	40.0	28.0	...	...	...	7.0	...	1.0	...	...	...

Grass Lake bog (4; Table 10, Fig. 11) is only 2 meters in depth but the bottom peat records dominance of Picea pollen and a very small amount of Abies which disappears at the next level above. Quercus and Pinus fluctuate in the middle part of the spectrum but the latter is the outstanding pollen in the upper layers. A slight decrease in the frequency of both genera in the

TABLE 10. PERCENTAGES OF FOSSIL POLLEN FROM GRASS LAKE BOG

Depth in meters	Abies	Picea	Pinus	Alnus	Betula	Corylus	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.
Surf.	...	...	44.0	...	2.0	...	12.00	...	...	32.0	6.0	4.0
0.20	...	...	50.0	1.0	6.0	...	27.0	1.0	1.0	7.0	6.0	1.0
0.40	...	...	47.0	...	5.0	1.0	30.0	...	...	5.0	11.0	1.0
0.60	...	...	41.0	2.0	2.0	1.0	42.0	...	1.0	7.0	4.0	...
0.80	...	1.0	40.0	2.0	2.0	2.0	32.0	...	3.0	9.0	8.0	1.0
1.00	...	...	29.0	2.0	2.0	2.0	41.0	1.0	2.0	11.0	8.0	2.0
1.20	...	...	58.0	...	...	...	25.0	...	...	6.0	4.0	7.0
1.40	...	8.0	56.0	2.0	...	...	9.0	1.0	...	5.0	9.0	10.0
1.60	...	15.0	40.0	5.0	...	...	8.0	...	...	10.0	10.0	12.0
1.80	2.0	50.0	26.0	6.0	...	...	10.0	...	...	2.0	4.0	....
2.00	3.0	65.0	13.0	1.0	...	3.0	11.0	...	...	...	4.0	....

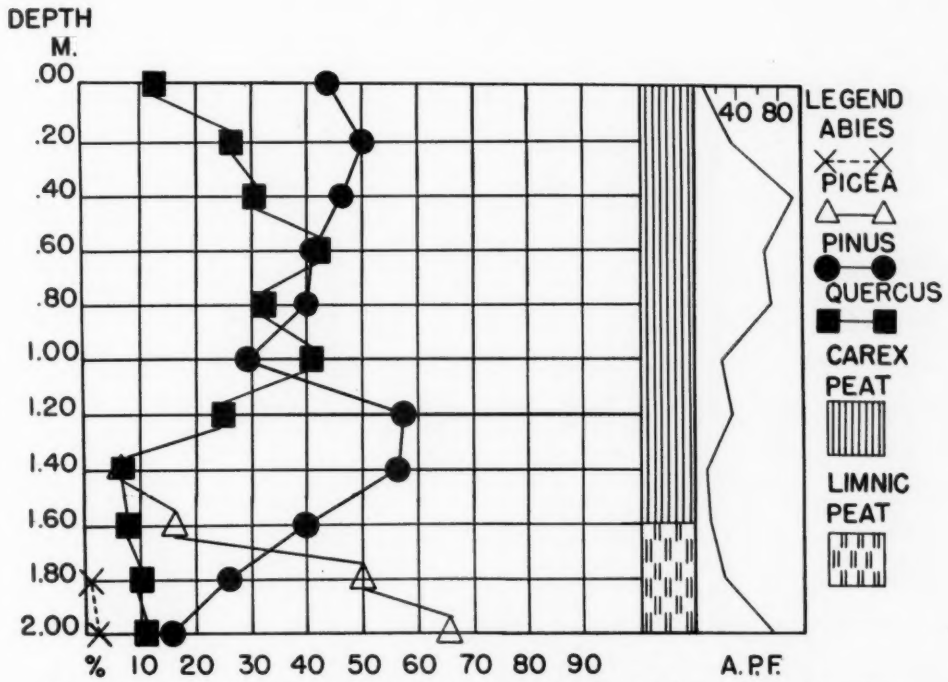

FIG. 11. Pollen diagram of Grass Lake bog. A.P.F.: absolute pollen frequency.

surface peat is probably to be correlated with the very marked increase in pollen of Gramineæ.

GROUP II. PROFILES BEGINNING WITH DOMINANCE OF PINUS AND QUERCUS

Tamarack Lake bog (2; Table 11, Fig. 12) in Anoka County may be considered the type spectrum of this group of four bogs. The materials of this deposit consist of about 5 meters of non-shell marl, 0.8 meter of limnic peat and above this a layer of carex peat 2 meters in thickness. This profile is similar to that of the Cedar Creek deposit in which a depth of 9 meters of marl was encountered. In the lowest level, pollen of Pinus represents more than 90 percent of the total grains counted, while the frequencies of Abies, Picea, and Quercus total less than 10 percent. Due to the fact that the pollen frequency of the marl dropped to less than 1 grain per square centimeter from the 6.2 meter to the 5 meter level, a break occurs in an otherwise continuous record. A single Quercus maximum of 42 percent appears at 3.4 meters and a trend toward a second is shown a little higher up at 2.8 meters. Throughout the remainder of the spectrum, Pinus is predominant.

It is striking that the pollen record of so deep a deposit should begin with Pinus as the dominant pollen while other more shallow bogs (Figs. 5, 6) show distinct Abies and Picea maxima. The bottom sediments were certainly obtained in this bog since the lowest sample of marl rested upon fine sand. A bog in Wisconsin reported by Hansen (1937) shows a similar spectrum in that the record begins with Pinus.

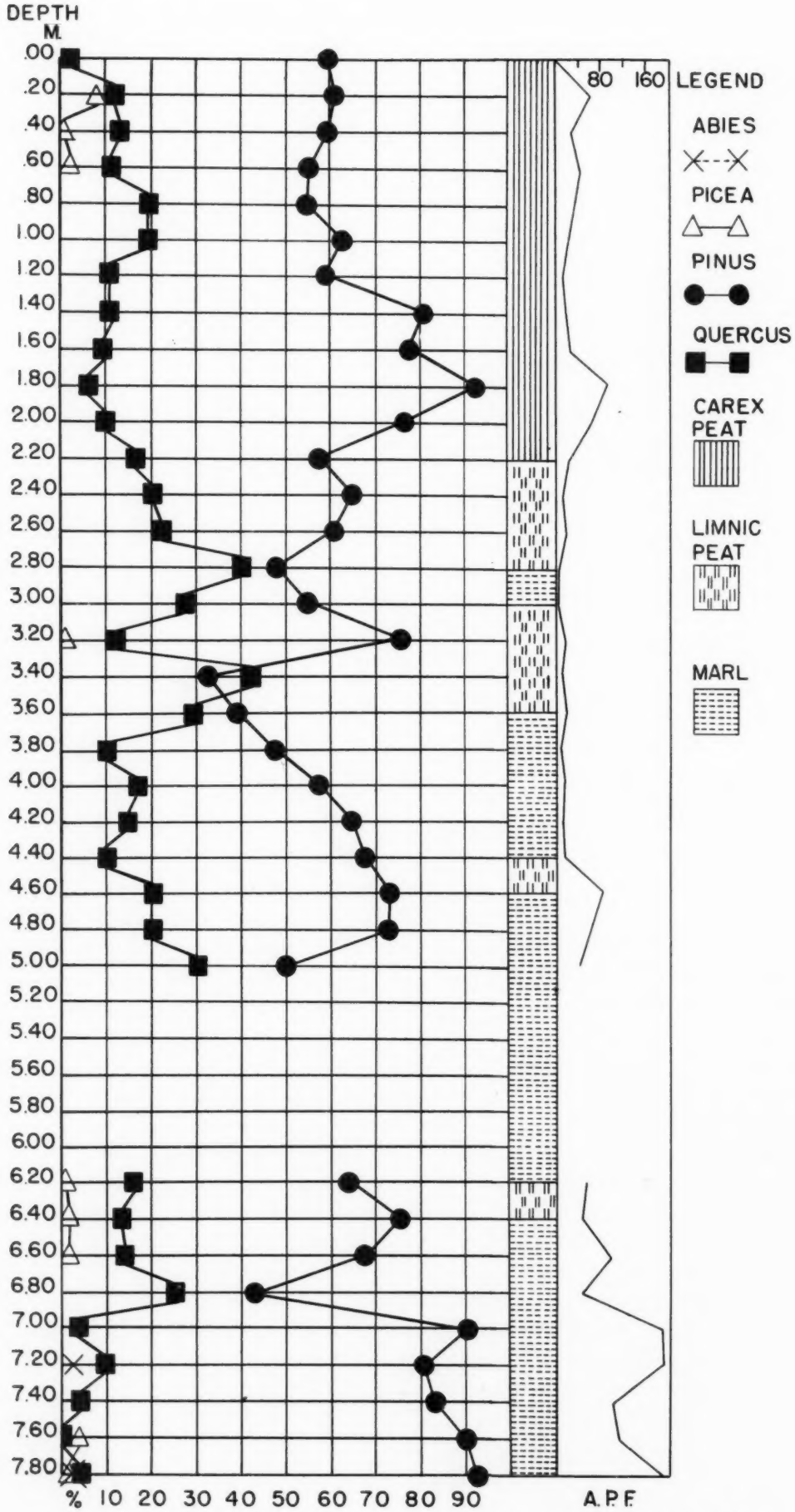

FIG. 12. Pollen diagram of Tamarack Lake bog. A.P.F.: absolute pollen frequency.

Bethel bog (7; Table 12, Fig. 13) is but 1.6 meters in depth and is the shallowest deposit investigated. Its pollen spectrum, however, is similar to that of the very deep profile just described. Pinus pollen is dominant at the bottom of the bog and continues in control throughout. The percentage of Quercus is slightly higher in the lower levels, while Abies and Picea are entirely absent. The meager showing of spruce pollen in the upper layers may be from black spruce growing on other bogs in the region.

Rabbit Lake bog (5; Table 13, Fig. 14) is similar to the Bethel deposit except that an extended period of Quercus dominance appears in the lower portion of the spectrum. At the 1-meter level, however, Pinus gains control

TABLE 11. PERCENTAGES OF FOSSIL POLLEN FROM TAMARACK LAKE BOG

Depth in meters	Abies	Picea	Pinus	Alnus	Betula	Corylus	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.	Nymphæaceæ
Surf.	....	....	60.0	....	....	....	2.0	....	....	12.0	14.0	12.0	....
0.20	....	9.0	61.0	....	....	1.0	12.9	....	....	12.0	4.0	1.0	....
0.40	....	1.0	59.5	3.0	2.5	0.5	13.5	....	0.5	14.5	4.0	1.0	....
0.60	....	2.0	56.0	4.0	3.0	1.0	11.0	....	11.0	14.0	9.0	....	....
0.80	....	....	55.0	2.0	3.0	....	19.0	....	....	16.0	4.0	1.0	....
1.00	....	....	62.0	....	2.0	3.0	19.0	....	....	6.0	6.0	2.0	....
1.20	....	....	59.0	....	3.0	....	11.0	....	2.0	15.0	7.0	3.0	....
1.40	....	....	81.0	2.0	1.0	....	11.0	....	....	1.0	4.0	....	....
1.60	....	....	78.0	1.0	3.0	....	9.0	....	....	4.0	4.0	1.0	....
1.80	....	1.0	92.0	....	1.0	....	6.0	....	....	....	....	1.0	....
2.00	....	1.0	77.0	....	....	....	10.0	....	....	5.0	7.0	....	....
2.20	....	....	58.0	....	2.0	....	17.0	....	....	7.0	14.0	2.0	....
2.40	....	....	65.0	2.0	1.0	1.0	20.0	....	....	3.0	7.0	1.0	....
2.60	....	....	61.0	....	1.0	....	22.0	....	....	3.0	6.0	7.0	....
2.80	....	....	48.0	....	3.0	....	40.0	....	....	3.0	2.0	4.0	....
3.00	....	....	56.0	....	3.0	....	28.0	....	....	6.0	5.0	2.0	....
3.20	....	1.0	75.0	1.0	....	....	12.0	....	....	4.0	3.0	4.0	....
3.40	....	....	32.0	2.0	....	....	42.0	....	1.0	3.0	18.0	2.0	....
3.60	....	....	39.0	3.0	1.0	....	29.0	....	2.0	8.0	15.0	3.0	....
3.80	....	....	48.0	4.0	4.0	....	10.0	....	....	10.0	20.0	4.0	....
4.00	....	....	58.0	....	....	....	17.0	1.0	1.0	9.0	12.0	2.0	....
4.20	....	....	65.0	....	2.0	....	15.0	....	....	5.0	10.0	3.0	....
4.40	....	....	68.0	....	2.0	....	10.0	....	....	3.0	15.0	2.0	....
4.60	....	....	72.0	....	....	....	20.0	....	....	1.0	5.0	2.0	....
4.80	....	....	72.0	....	2.0	....	20.0	....	....	2.0	4.0	....	....
5.00	....	....	50.0	....	2.0	....	30.0	1.0	....	5.0	8.0	4.0	....
5.20	....	....	....	....	....	....	....	....	....	....	....	....	....
5.40	....	....	....	....	....	....	....	....	....	....	....	....	....
5.60	....	....	....	....	....	....	....	....	....	....	....	....	....
5.80	....	....	....	....	....	....	....	....	....	....	....	....	....
6.00	....	....	....	....	....	....	....	....	....	....	....	....	....
6.20	....	1.0	64.0	....	....	....	16.0	1.0	....	8.0	6.0	4.0	....
6.40	....	2.0	76.0	....	....	....	13.0	....	3.0	4.0	1.0	1.0	....
6.60	....	2.0	68.0	1.0	1.0	....	14.0	....	....	7.0	7.0	....	....
6.80	....	....	42.0	1.0	4.0	....	25.0	....	5.0	8.0	12.0	5.0	1.0
7.00	....	....	90.0	....	3.0	....	4.0	1.0	1.0	3.0	1.0	....	....
7.20	1.0	....	81.0	....	2.0	....	9.0	2.0	1.0	3.0	....	....	....
7.40	....	....	83.5	....	1.0	....	4.5	3.0	2.5	3.5	0.5	0.5	....
7.60	....	2.5	91.0	....	2.0	....	1.0	0.5	0.5	1.5	1.0	....	....
7.80	1.0	2.0	92.0	....	2.5	....	2.5	....	....	1.5	1.0	....	....

and dominates most of the remainder. A sharp decrease in frequency of its pollen occurs at the surface which is probably due to the increase in pollen of Compositæ and Amaranth-Chenopod (Table 13).

Clear Lake bog (14; Table 14, Fig. 15) is similar to Tamarack Lake. Pinus is the outstanding pollen in the spectrum except at the surface where it shows a very marked decrease to 16 percent, while the frequency of Composite

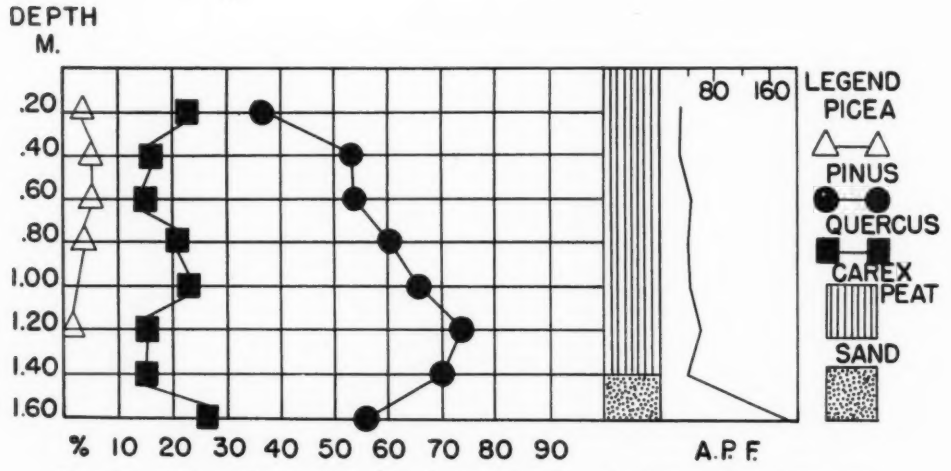

FIG. 13. Pollen diagram of Bethel bog. A.P.F.: absolute pollen frequency.

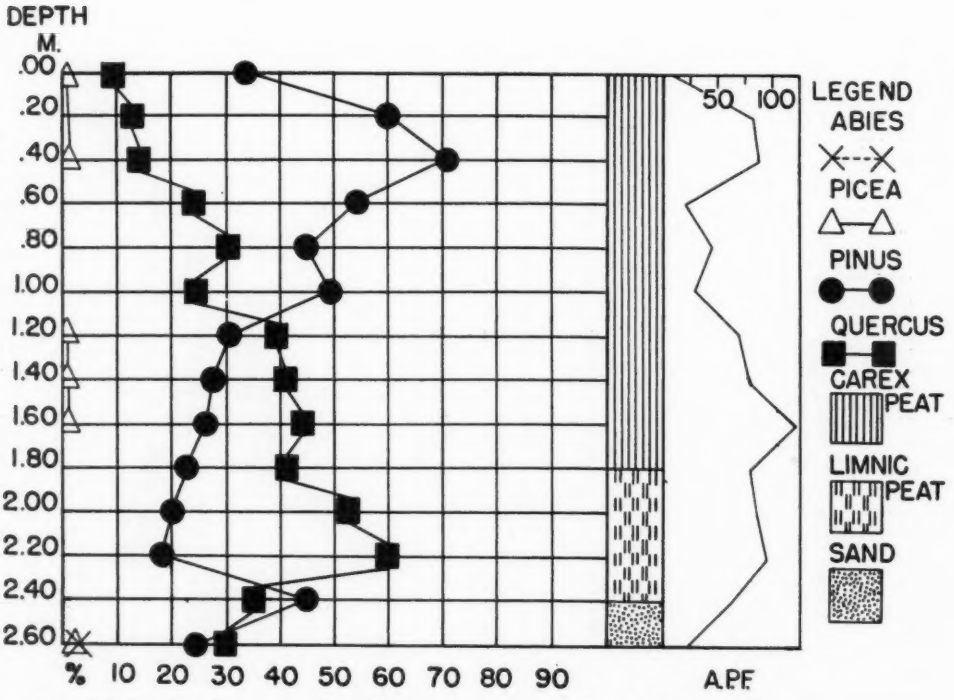

FIG. 14. Pollen diagram of Rabbit Lake bog. A.P.F.: absolute pollen frequency.

TABLE 12. PERCENTAGES OF FOSSIL POLLEN FROM BETHEL BOG

Depth in meters	Picea	Pinus	Alnus	Betula	Corylus	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.
0.20.....	4.0	37.0	...	4.0	...	22.0	...	...	16.0	9.0	8.0
0.40.....	6.0	52.0	1.0	5.0	...	16.0	5.0	...	5.0	9.0	1.0
0.60.....	6.0	53.0	3.0	9.0	...	14.0	2.0	1.0	4.0	8.0	...
0.80.....	4.0	60.0	...	4.0	...	21.0	...	...	1.0	8.0	2.0
1.00.....	...	66.0	...	5.0	...	22.0	...	...	4.0	3.0	...
1.20.....	2.0	73.0	...	3.0	...	16.0	2.0	...	3.0	...	1.0
1.40.....	...	70.0	...	2.0	2.0	16.0	2.0	...	5.0	2.0	1.0
1.60.....	...	56.0	...	2.0	1.0	27.0	1.0	...	7.0	5.0	1.0

TABLE 13. PERCENTAGES OF FOSSIL POLLEN FROM RABBIT LAKE BOG

Depth in meters	Abies	Picea	Pinus	Alnus	Betula	Corylus	Acer	Quercus	Tilia	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.	Nymphæaceæ
Surf.....	....	1.0	33.0	2.0	2.0	1.0	....	9.0	....	....	15.0	24.0	13.0	....
0.20.....	....	....	60.0	5.0	....	....	....	12.0	....	....	15.0	4.0	4.0	....
0.40.....	....	1.0	71.0	....	2.0	....	....	13.0	....	....	10.0	3.0	1.0	....
0.60.....	....	....	53.0	....	3.0	....	....	23.0	1.0	3.0	8.0	9.0	2.0	....
0.80.....	....	....	44.0	....	6.0	3.0	....	30.0	....	2.0	18.0	7.0	1.0	....
1.00.....	....	....	49.0	....	4.0	....	....	24.0	....	....	25.0	8.0	....	....
1.20.....	....	1.0	31.0	3.0	3.0	....	....	39.0	2.0	1.0	16.0	6.0	1.0	....
1.40.....	....	1.0	28.0	3.0	3.0	....	....	41.0	....	....	14.0	7.0	3.0	....
1.60.....	....	1.0	27.0	3.0	3.0	3.0	....	44.0	....	....	13.0	6.0	....	2.0
1.80.....	....	....	22.0	1.0	2.0	....	....	41.0	2.0	....	9.0	16.0	7.0	....
2.00.....	....	....	20.0	2.0	3.0	....	....	52.0	1.0	1.0	7.0	15.0	....	....
2.20.....	....	....	18.0	2.0	4.0	....	....	59.0	....	....	8.0	10.0	....	....
2.40.....	....	....	44.0	....	3.0	....	....	37.0	0.5	....	8.0	6.0	2.5	....
2.60.....	2.5	2.0	24.5	0.5	3.0	....	2.5	29.0	1.5	3.5	11.0	16.0	4.0	....

TABLE 14. PERCENTAGES OF FOSSIL POLLEN FROM CLEAR LAKE BOG

Depth in meters	Picea	Pinus	Alnus	Betula	Quercus	Ulmus	Gramineæ	Compositæ	Amaranth-Chenopod.
Surf.....	....	16.0	4.0	6.0	5.0	....	14.0	41.0	....
0.20.....	....	69.0	4.0	6.0	10.0	....	19.0	2.0	....
0.40.....	5.0	80.0	....	....	8.0	....	6.0	1.0	....
0.60.....	2.0	75.0	....	5.0	7.0	....	9.0	2.0	....
0.80.....	....	80.0	....	....	5.0	....	6.0	6.0	3.0
1.00.....	4.0	86.0	....	....	2.0	4.0	18.0	2.0	4.0
1.20.....	....	80.0	....	....	....	....	15.0	5.0	....
1.40.....	....	....	....	....	....	....	....	....	....
1.60.....	....	....	....	....	....	....	....	....	....
1.80.....	....	....	....	....	....	....	....	....	....
2.00.....	....	....	....	....	....	....	....	....	....
2.20.....	....	....	....	....	....	....	....	....	....
2.40.....	....	92.0	2.0	....	1.0	....	5.0	....	....
2.60.....	0.5	78.5	....	0.5	1.5	....	18.0	1.0	....

pollen increases to 41 percent. A break in the record occurs from the 2.4- to the 1.2-meter level, due to the low pollen frequency of the limnic peat.

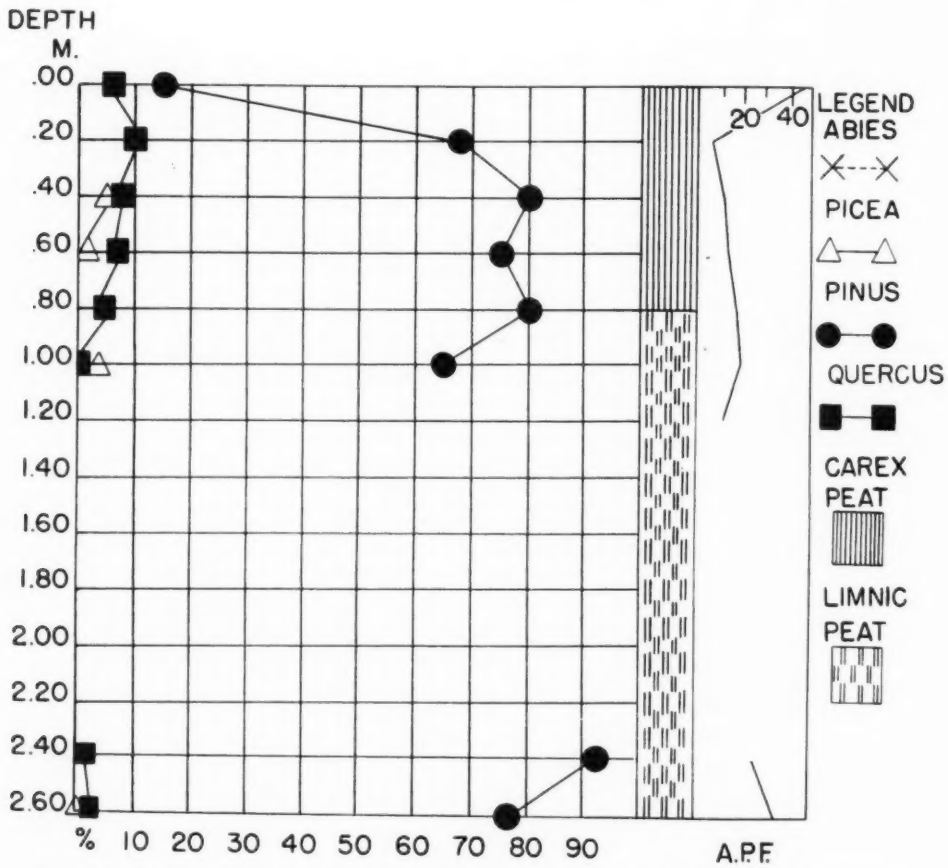

FIG. 15. Pollen diagram of Clear Lake bog. A.P.F.: absolute pollen frequency.

DISCUSSION

Many students of pollen analysis in this country have followed the practice of drilling only the deepest bogs, maintaining that the earliest records may be obtained only in this way. Wilson believes, however (1938), that the smaller and shallower bogs, in all cases less than one acre in area and often but a few inches deep, give as complete a record as the deeper deposits. In his own work he has avoided sampling the deeper bogs, asserting that they present many complex problems in sedimentation.

In the present study, the fourteen bogs drilled include both deep and shallow deposits, varying in depth from 1.6 meters to more than 11 meters. The depths of the complete series are shown in Table 15.

Pollen spectra of ten of the fourteen bogs are theoretically complete in that they show initial dominance of Abies and Picea or of Picea alone at the bottom. In the other four the record begins with dominance of Pinus,

the above two genera being barely suggested at the bottom or not present there, and such a profile may be said to give an "incomplete" record. Division of the series into "shallow" and "deep" classes must necessarily be arbitrary and will not be attempted. It appears from the table, however, that three of the four shallowest bogs have incomplete records, while all the others are complete except one, which is next to the deepest. The evidence, as far as it goes, seems to indicate that Wilson's trust in shallow bogs is not justified, and that the deeper ones are more likely to give a complete picture of post-glacial vegetational history.

TABLE 15. DEPTH OF BOGS AND COMPLETENESS OF PROFILE
(C: complete; I: incomplete)

Bog	*Depth*	
Bethel	1.6 m.	I
Grass Lake	2.0 m.	C
Rabbit Lake	2.6 m.	I
Clear Lake	2.6 m.	I
Princeton	3.4 m.	C
Rice Lake	4.4 m.	C
Karmel	4.8 m.	C
Elk River	4.8 m.	C
Coon Lake	5.0 m.	C
Ham Lake	5.2 m.	C
Linwood	6.0 m.	C
Coon Creek	7.0 m.	C
Tamarack Lake	7.8 m.	I
Cedar Creek	11.0 m.	C

It is further indicated that the common practice of attempting to interpret vegetational and climatic history from a single bog profile in an area is faulty in that there is no assurance that the particular one studied gives a complete record. Dependence upon the shallow Rabbit Lake bog alone, for example, or the deep Tamarack Lake bog, would lead to erroneous conclusions. The only safe method is to investigate a group of bogs close enough together so that the climatic sequence must be the same for all; and this group, so far as possible, should be confined to a physiographic formation uniform in origin and age. The series selected fulfills these requirements to a satisfactory degree.

Presumably the ten with "complete" records provide the most adequate vegetational history of the region, and these will therefore be first considered, afterward, the problem presented by the bogs with "incomplete" records will be discussed.

VEGETATIONAL AND CLIMATIC HISTORY AS DISCLOSED BY THE BOGS WITH COMPLETE RECORD

Combined evidence from the bogs of this group indicates spruce-fir forest as the first type leaving a record. Five of the profiles show Abies as the first dominant, followed by Picea; three show Picea dominating at first with Abies in minor quantity and decreasing. In two cases Abies reaches a maxi-

mum after the decline of spruce. These variations might well be due to differing successional changes related to local environmental differences. There is agreement in general here with records discovered by other workers as noted in the historical summary.

Bogs of this group agree fairly well in history after the practical disappearance of Abies and Picea. Curves of pine and oak cross and recross, but the former dominates more or less and in some cases, decisively so. Valuable local confirmation is found in the study by Voss (1934) at Bald Eagle, near the boundary of Washington and Ramsey counties in Minnesota. Located upon drift of the Grantsburg Sublobe, it must be of approximately the same age as the bogs on the Anoka Sand plain. Its spectrum indicates that the postglacial plant succession has been Abies-Picea to Pinus-Quercus, although the record throughout most of the latter period is omitted from the diagram due to the low pollen frequency of the peat. There is thus agreement in general with other recorded bog profiles of the northern stations and therefore a history different from that indicated by more southern bogs in which deciduous genera show a more pronounced dominance (see historical summary).

In interpreting pollen profiles, the most rational view seems to be that of Aario (1932) who holds that the only significant indications of climatic change are appearance and disappearance of genera, and that relative fluctuations are not to be relied upon.

In the history of the Anoka Sand Plain as indicated by these ten profiles, the only significant events are initial appearance of Abies and Picea and their subsequent practical disappearance. Fluctuations in genera which continue through the record, such as pine and oak, are inconclusive unless they can be traced from section to section. This cannot be done, therefore there is no valid evidence for climatic change since the disappearance of Abies and Picea. The facts do not disprove climatic changes but they throw no light on the problem. It is suggested that local successional changes, perhaps secondary, due to fire or other causes, may account for the alternation of pine and oak.

There is indicated, therefore, a single major progressive climatic change: from conditions favoring continental glaciation to conditions bringing about its disappearance. During this period of transition, the ice melted away, Abies and Picea established dominance and held it for a relatively brief period, and were succeeded by dominance of pine and oak with other angiosperm species in minor amount. Since the disappearance of spruce and fir, no climatic change of major magnitude is indicated.

It was stated in the historical summary that certain workers find evidence for postulating a period of maximum warmth during the time represented by the middle of the profiles investigated. A general increase in grass-Amaranth-Chenopod pollen in certain of the northern bogs has been con-

sidered by Sears (1935) to indicate a xerothermic period. Whatever evidence there may be in the present data to indicate such a climatic change should in all fairness be presented. Accordingly, a statistical analysis was made of the percentages of this complex (grass-Amaranth-Chenopod), by periods, using the shift from spruce-fir to pine-deciduous as a base, and extending to the surface. Only the ten bogs with complete record were utilized. Since these differed greatly in depth, an attempt was made to adjust all to an approximate standard time-scale, based upon the profile at Coon Creek bog, which shows the clearest record of the basal shift. In this the pertinent portion of the profile is six meters deep, and the standard time-scale was accordingly divided into six units. For each of the other bogs the adjustment was made by multiplying the intervals between sampling depths by a factor obtained by dividing the standard six meters by the depth of the bog. In this way the shallower profiles were stretched out and the deeper ones shortened to conform with the standard.

Summation of percentages of grass-Amaranth-Chenopod pollen from the ten complete bogs supplied points which were used to construct a graph, plotting percentage against time. The mean of all the points falling within each time division was taken and when these were again plotted a curve showing the average of the ten bogs was obtained (Fig. 16).

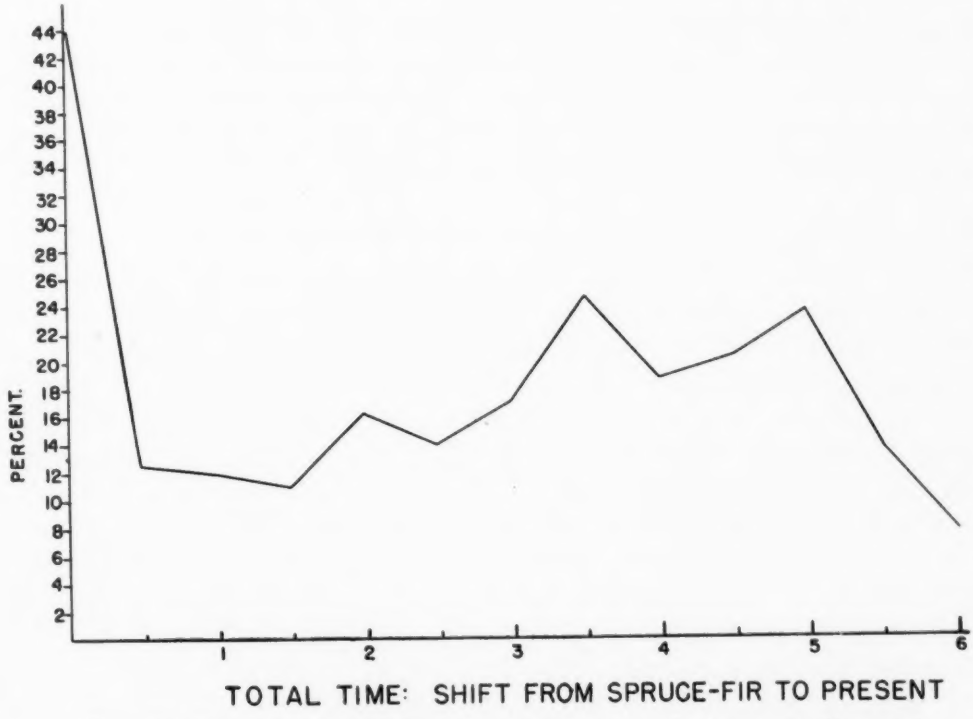

FIG. 16. Curve of the combined percentages of grass-Amaranth-Chenopod pollen based on data from 10 bogs. Total time is an arbitrary time scale using the shift from spruce-fir as a marker.

The highest percentage (44 percent) appears at the surface and may be attributed to an increase of pollen of this complex due to disturbance as has been found in the surface layers by other workers. The remainder of the curve, after irregularities have been smoothed out, seems to point to a rather general increase of pollen of this group at some time during the middle period. It must be kept in mind that these percentages are only relative and in no case does this complex show a maximum over pollen of pine or oak. Whether or not this increase in the grass complex is significant enough to indicate a climatic change is left an open question.

The presence of oak pollen at the bottom of the profiles, and of other angiosperm genera at very low levels, is significant. If the occurrence of pollen were sporadic, it might have been blown from a long distance, but in the case of oak at least it seems too consistently present for this. The data strongly indicate the presence of at least a few angiosperm trees in the immediate region, suggesting that some species entered the region almost as soon as the pioneer conifers. Such an hypothesis should be easy to accept in view of the nearness of regions which might have served as sources of seed (Cooper, 1938). Areas undisturbed since Kansan time lay beyond the limits of the Wisconsin ice advance but sixty-five kilometers from the Anoka Sand Plain; the Driftless Area is not much farther away. Moreover, there is strong confirmation in unpublished studies of C. O. Rosendahl on wood and other fossil material found in silts of Lake Agassiz. Furthermore, abundance of pollen at depths of twenty and forty centimeters in the sand at the bottom of three sections in the present study, indicating that pollen was being deposited while sediments were still being washed or blown into the lakes, suggests very early establishment of vegetation in the vicinity.

THE PROBLEM OF THE BOGS WITH INCOMPLETE RECORD

Four sections in which the profile begins with dominance of pine and oak strongly suggest a truncated record with the lower portion missing. Finding these side by side with a larger series showing complete records presents a problem which still awaits solution. These four profiles are very similar to that of the Dells bog of Hansen (1937), who explains lack of Abies and Picea on the basis of late origin of basin, and compares it with the nearby Baraboo bog on much older terrain which shows a complete record. In this case geologic evidence supports Hansen's conclusions. Such an explanation will not hold in the case of the Anoka Sand Plain, since all the basins are of closely similar age. It may be remarked, that, judging from results of the present study, it is possible that if Hansen had investigated other bogs under the same conditions as obtain at the Dells bog, he might have discovered that the latter is an exceptional case. Moreover, Voss (1937) found the same conifers in bogs located on Cary and Tazewell drift in Illinois differing some 8,000 years in age.

One possible explanation, for Minnesota bogs at least, is that certain ice blocks remained unmelted much longer than others, so that the resulting pits came into being much later. In the meantime, Abies and Picea attained dominance and disappeared from the vicinity, so that the first adjacent vegetation was Pinus-Quercus. This hypothesis would require persistence of buried ice for a number of centuries.

It is possible that some of the incomplete bogs could have formed later than the complete bogs due to shifting sands during early postglacial time. Detailed study of the bottom sands of the "incompletes" might reveal the missing Abies and Picea maximum and careful investigation of these particular pits with regard to size, form and probable physiographic history might also suggest a clue. At present, the problem must be left unsolved.

SUMMARY

Fourteen bogs drilled on the Anoka Sand Plain include both deep and shallow deposits, varying in depth from 1.6 meters to more than 11 meters. The pollen analyses show that there is a rough correlation between depth and completeness of record.

Pollen spectra of ten of the bogs indicate that Abies and Picea were the first dominant trees in the region after ice recession, and that this pioneer forest was superseded by Pinus-Quercus, while four show that the postglacial plant succession had reached the Pinus-Quercus stage when they came into being.

Overwhelming abundance of Abies and Picea followed by their practical disappearance is the most significant event recorded in the spectra and indicates a major climatic change.

Fluctuations in Pinus and Quercus through the upper two thirds or more of the profiles have no certain climatic significance and may be due to local causes. Therefore, no climatic changes are indicated since the disappearance of Abies-Picea. In general, the recent increase in spruce at the upper levels is probably due to the presence of this tree on the bog or in the immediate vicinity.

A statistical analysis of the combined percentages of grass-Amaranth-Chenopod pollen based on data from the ten complete bogs shows that there is some evidence for a general increase of this group in the middle of the profiles. Interpretation of this curve must await further investigation.

Consistent occurrence of Quercus at the bottom of all profiles and general presence of other angiosperms at very low levels in some strongly suggests that certain deciduous genera came into the region almost as soon as the pioneer conifers.

These studies show that the group method gives more reliable data than the single-bog plan, unavoidable in reconnaissance study, in that it avoids, to a reasonable degree, the danger of basing conclusions on exceptional cases.

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A LIMNOLOGICAL INVESTIGATION OF THE MICROSCOPIC BENTHIC FAUNA OF DOUGLAS LAKE, MICHIGAN

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A LIMNOLOGICAL INVESTIGATION OF THE MICROSCOPIC BENTHIC FAUNA OF DOUGLAS LAKE, MICHIGAN

INTRODUCTION

Previous investigations on bottom faunas have been concerned with the larger organisms with only incidental consideration, or more often, no mention at all, of the microfauna. In his paper on the bottom fauna of Lake Simcoe, Ontario, Rawson (1930) included some observations on the microfauna, listing 68 species and indicating their depth distribution. Bigelow (1928) described the ecological distribution of microscopic organisms in Lake Nipigon, Ontario, listing the organisms which he found in the "inshore bottom systasis" of the "bottom association." He listed 28 animals and 16 plants in the "ooze-film assemblage" and 18 animals in the "associated ooze-film assemblage." Baker (1918) listed 10 Cladocera, 1 copepod and 5 Naididae from the bottom deposits of Oneida Lake, New York. Juday (1908) found several microscopic animals living under anaerobic conditions in the profundal region of Lake Mendota, Wisconsin. Adamstone and Harkness (1923) and Adamstone (1923; 1924) included mention of microfauna in the bottom deposits of Lake Nipigon, Ontario. Several researches on European Lakes should be mentioned. In every instance they are general studies of bottom fauna, with certain microfauna included. Investigations on Swiss alpine and subalpine lakes which included the microfauna are those of Zschokke (1906; 1910), Brehm (1909), Fehlmann (1912), Hofsten (1912), Schmassmann (1923), and Borner (1917; 1928). These papers are primarily zoogeographical, with emphasis on the distribution of "glacial relicts." The work of Deksbach (1925) on several Russian lakes included certain microfauna.

In this investigation the writer has attempted to work out the microscopic benthic fauna of one lake, both qualitatively and quantitatively; to determine the distribution within the lake; and to study the adaptations of these organisms to their environment. The microscopic benthic organisms form an important link in the chain of those organisms which make available the food materials that are present in the bottom deposits. Some of them feed on the bacteria of the bottom deposits; others both on the bacteria and directly on bottom-deposit materials. These microscopic bottom organisms, in turn, are fed upon by the macroscopic bottom animals and certain of the bottom feeding fishes. This investigation, then, deals with a long-neglected group of organisms which are of fundamental importance in the biological productivity of a lake.

This work covered the summers of 1933, 1934, 1935, 1936, and 1937, all collections being made during June, July and August, with the exception

of one series taken in October, 1937. It was done on Douglas Lake, Cheboygan County, Michigan. Morphometric, physico-chemical, and biological data concerning this lake have been presented in previous papers from the University of Michigan Biological Station (Welch, 1927; Welch and Eggleton, 1932; Eggleton, 1931; Miller, 1936). Eggleton defined the limits of the

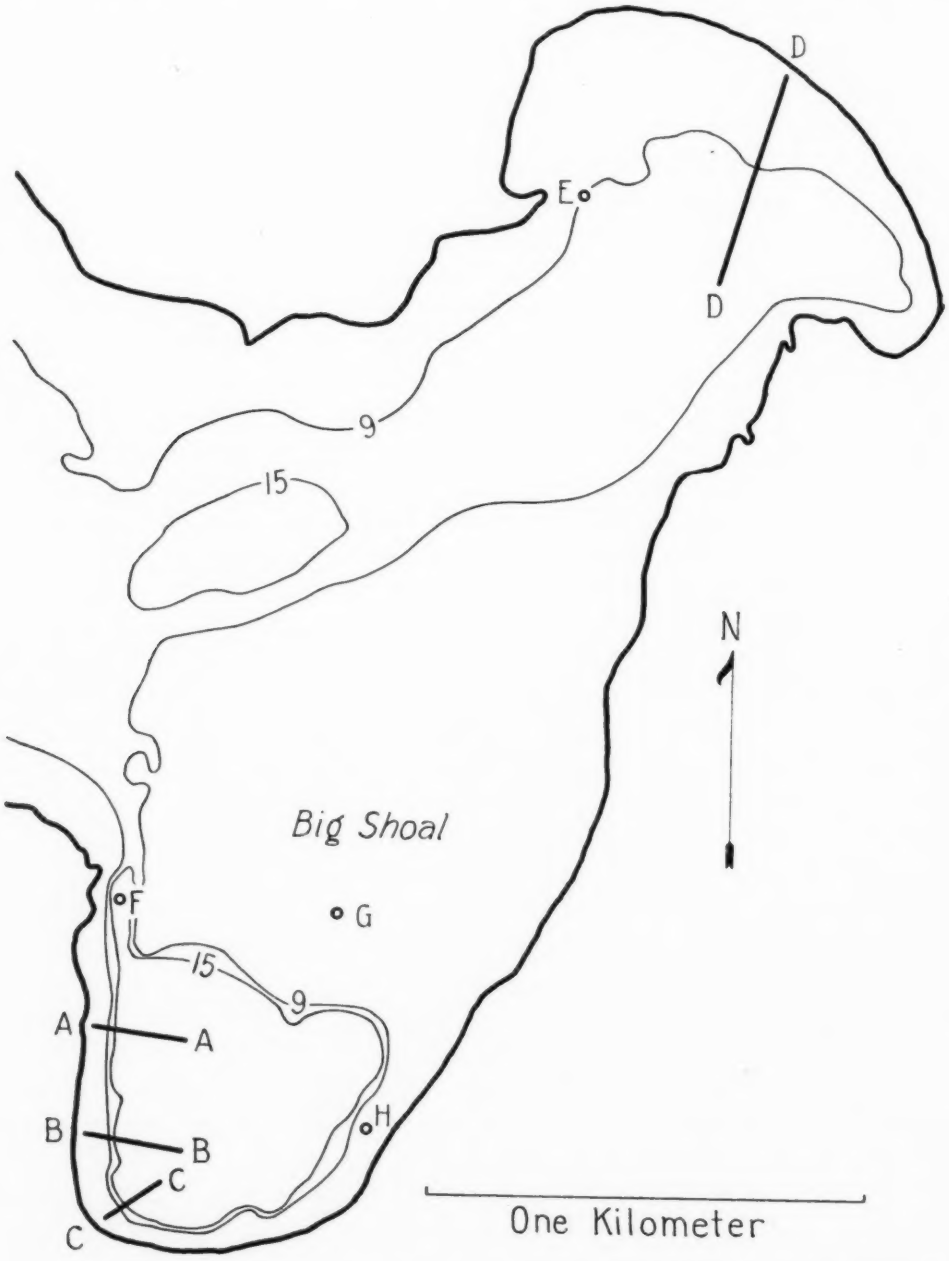

FIG. 1. Map of the east end of Douglas Lake showing the transects and most of the stations used. Nine-meter and 15-meter contour lines indicate the extent of the littoral, sublittoral and profundal regions.

bottom zones of Douglas Lake as follows: littoral, 0-9 m.; sublittoral, 9-15 m.; profundal, 15-28 m.

Figure 1 shows the position of the transects and most of the stations used. During the first two summers, samples were taken from several stations in various parts of Douglas Lake. It was soon apparent that more could be gained by an intensive study of one region than by studying less frequent collections from many regions in the lake. After 1934, all collections were made from transects AA and BB. Two stations not shown in Fig. 1 were used in 1934.

In all, 80 collections of bottom samples have been examined, 27 of which were quantitative and made with the vertical core sampler. Most of the qualitative samples were taken with the ooze sucker.

Four plankton collections served to determine seasonal distribution of adult and immature *Cyclops bicuspidatus,* an encysted stage of which was found in the bottom deposits. These samples were secured by making vertical hauls from bottom to surface by means of a plankton net equipped with No. 20 silk bolting cloth.

Several vertical series of physico-chemical records were secured by the writer; others were made available to him through the courtesy of associates.

APPARATUS AND METHODS

Bottom Samplers

The ooze sucker used in this investigation is essentially like that devised by Rawson (1930). In his description, the screen over the mouth of the funnel is designated as "a coarse metal screen, 150 meshes to the inch." Obviously, he meant either 15 meshes to the inch or 150 meshes to the square inch. The ooze sucker used in this investigation (Pl. I, Fig. 14, 15) has a 20-to-the-inch mesh screen. The plates on the arms which compress the bulb are larger than those on Rawson's apparatus, thus increasing their effectiveness.

This ooze sucker was the most satisfactory instrument for qualitative collections. However, it is not suitable for quantitative work since: (1) it disturbs the finely divided ooze as it settles onto the bottom; (2) it collects only those organisms near the surface of the deposits; and (3) its efficiency is probably different on muck bottom and on sand bottom.

For quantitative sampling a vertical core sampler (Pl. I, Fig. 19, 20), made by the Foerst Mechanical Specialties Company, was used. It consists of a brass tube with a steel nose on the lower end and a weight and valve on the other. The valve permits free passage of water through the sampler as it descends, and closes automatically as the instrument is hauled up. A glass tube fits within the outer tube. The sampler is permitted to fall swiftly through the water and imbed itself in the bottom. It is then hauled to the surface, a cork placed in the bottom of the sampler, and the glass tube with

the core of bottom deposits removed by unscrewing the steel nose. The overall length of the sampler is 60 cm. Each glass tube has a length of 48.4 cm. The inside diameter of the steel nose and of the glass tube is 2.2 cm. The area sampled is 3.8 sq. cm. Considerable difficulty was experienced in attempting to make the vertical core sampler function on sand bottom since it did not penetrate deep enough to hold the sample as it was hauled up. An additional weight (Pl. I, Fig. 20a) was designed in the form of a collar which slipped over the outside of the brass tube. This collar consists of two pieces of iron pipe, one within the other, the space between them being filled with lead. This collar is 25.6 cm. long; has an inside diameter of 3.4 cm.; an outside diameter of 6.0 cm.; and weighs about 4.5 kg. It is held in place on the upper end of the brass tube by hose clamps. Equipped in this manner (Pl. I, Fig. 20) the sampler penetrates hard sand bottoms to a depth of about 15-20 cm. Thus sand cores are usually retained while the sampler is hauled to the surface, even from water depths of 12 m. or more. The field case used in carrying extra glass tubes and the cores is shown in Plate I, Fig. 16.

Qualitative Examinations

Material collected with the ooze sucker was examined under a low-power binocular microscope. The magnification ranged from 12 to 39 diameters. As specimens were found they were removed by means of a capillary pipette, transferred to a microscope slide, and examined under a compound microscope.

To facilitate the isolation of larger forms, material collected with the ooze sucker was often screened with a 100-mesh-to-the-inch Tyler screen (mesh size, 0.15 mm.). The washing out of the finer detritus and the resulting concentration made it possible to examine much larger samples. Obviously, this procedure resulted in loss of most Protozoa and Rotatoria and of some Nematoda. However, these organisms were secured from unscreened samples.

Practically all collections were examined alive. In the bottom-deposit materials, active organisms are much easier to distinguish than preserved ones. Qualitative collections from several stations were sometimes made on the same day. The resulting samples were then stored in a refrigerator and examined as soon as possible.

It was felt that much could be gained by collecting these qualitative samples in a systematic manner. Starting in June, 1935, series of collections were made along transects up the slope of the basin. Transects AA and BB (Fig. 1) were used. Three such series of qualitative samples were studied in 1935, and one in 1936.

Quantitative Examinations

Quantitative methods were devised using a vertical core sampler as the basic instrument. To facilitate removal of material from the cores for quan-

titative examination and to study the vertical distribution of organisms in bottom deposits, it was necessary to work out a method of sectioning the cores. The method is illustrated in Plate I, Fig. 17, 18. A properly fitted piston (b), made from part of a rubber stopper, is inserted at the lower end of the glass tube. A rubber cup (a), 6 cm. in diameter, 3 cm. high, with a hole 2.2 cm. in diameter in the bottom, encircles the tube with the rim of the cup about 2 cm. below the top. The result is a water-tight trough around the upper end of the tube. Clear water above the bottom deposits is siphoned off. The piston and the core of bottom deposits is pushed to the upper end of the tube by inserting a rod, graduated in centimeters, below the piston. The first cm. of bottom deposits is forced up above the end of the tube, part of it spilling over and the rest of it being scraped off into the cup. This material is removed from the cup by means of a small bulb syringe, and the cup washed with tap water. The next cm. of bottom deposits is then pushed up above the end of the tube and removed in the same way. The base (Pl. I, Fig. 17, 18, c), which serves as a support for the glass tube during the process of sectioning the core, is made from a rubber suction cup (diameter, 11 cm.).

In the preliminary quantitative work, a single core (3.8 sq. cm. area) was taken in each collection. However, since distribution of microscopic bottom organisms is probably not uniform, it was felt that a more correct measure of the population could be obtained by taking several samples, mixing similar strata from each sample, and then counting the organisms in some fraction of this aggregate sample. In most instances, five cores (19 sq. cm. total area) taken at random constituted a collection. Each core was sectioned, usually into the following strata: 0-1 cm. (i.e., the upermost centimeter of the bottom deposits); 1-2 cm. (i.e., the second centimeter of bottom deposits); 2-3 cm.; 3-4 cm.; 4-5 cm.; 5-8 cm.; 8-11 cm.; 11-14 cm.; 14-17 cm.; 17-20 cm. The 0-1 cm. stratum from all of the five cores was mixed together; the 1-2 cm. stratum from all of the five cores was also mixed; and in a like manner aggregate samples were prepared for the other strata. Aggregate samples of the first five strata were diluted to 100 ml. volume with filtered water. After thorough mixing, 20 ml. of the aggregate sample were removed for direct examination. The remaining 80 ml. were screened, using a 100-mesh Tyler screen, and the screenings retained for examination. In this way, smaller organisms (Protozoa, Rotatoria, and minute nematodes) were counted in one fifth of the sample and larger, usually less numerous, organisms counted in the whole aggregate sample. All material from the aggregate samples of the lower strata (5-8 cm., 8-11 cm., 11-14 cm., 14-17 cm., 17-20 cm.) was screened with a 100-mesh Tyler screen, and the screenings retained for examination. Since preliminary examination showed the absence of these smaller animals below the five-centimeter level, only screened samples from the lower strata were examined.

Since most of the counting was done on living material, a counting chamber no wider than the field of the binocular microscope was essential. The most satisfactory chambers were made by placing strips of adhesive tape on frosted glass lantern-slide plates (10.2 by 8.2 cm.) and coating the tape with paraffin. Four or five chambers, 7-8 mm. by 9 cm., were thus arranged on a single plate. The frosted glass resulted in more evenly distributed illumination and less glare. The chambers were placed on the frosted side of the glass.

Physico-chemical Methods

Physico-chemical determinations involved the use of a Negretti and Zambra reversing thermometer; a modified Kemmerer water sampler; and a pH colorimeter and indicators purchased from the LaMotte Chemical Products Co. Chemical analyses for dissolved oxygen, free CO_2, and alkalinity were made according to the procedures outlined in Standard Methods for the Examination of Water and Sewage (7th edition, 1933).

NATURE OF BOTTOM DEPOSITS ALONG TRANSECT AA

Along transect AA sand bottom extends lakeward from the shore line to a water depth of about 12.5 m., and along transects BB and CC to a water depth of about 9 m. Deposits from these depths out to the deepest regions are soft black ooze.

Core samples taken at 8 m. water depth along transect AA consisted of an upper layer of fine ooze (organic detritus) about 4 mm. thick, and below this of clean, hard-packed sand.

Cores taken from bottom deposits under 11 m. of water showed at the top a layer of organic detritus about 1 cm. thick; then followed a stratum of sand about 6 cm. thick blackened with considerable organic detritus; and, finally, there was a layer of homogeneous grey marl at least 14 cm. thick. As the cores did not extend through this layer of marl, no precise statement can be made as to its thickness.

Cores taken at 12 m. water depth showed 1 cm. of ooze on top, then about 10 cm. of blackened sand, and below this 8 cm. of clean sand. The line between the blackened sand and the clean sand was not sharp.

Cores from 14 m. water depth showed 18 cm. of black ooze, which is as far as the sampler penetrated. The first 2 cm. of this deposit were quite liquid. Below 2 cm. the deposit became more solid until at the 5 cm. level and below it held its shape when pushed above the end of the glass tube. The nature of this black ooze was described by Eggleton (1931).

Cores taken at 17 and 20 m. water depth were similar to those from 14 m., except that they were not as solid, the sampler penetrating to a depth of 20 to 25 cm. Below the 8 cm. level the deposit was solid enough to stand by itself when pushed above the end of the tube.

The prevailing idea that there is immediately above the bottom a stratum

of water which is always turbid due to detritus in suspension should be questioned as far as the Douglas Lake situation is concerned. When proper care was used in removing the glass tubes from the sampler, the superimposed water was clear. The transition from clear water to bottom deposits was an abrupt one. The upper deposit was not solid enough to support objects, yet it certainly could not be classed as turbid water.

LIMITS OF PROBLEM

In this investigation only *microscopic benthic animals* have been considered. As there is no distinct line of demarcation between macroscopic and microscopic organisms, the following groups have been arbitrarily considered as macroscopic and hence outside the limits of this problem: Mollusca, Insecta, Malacostraca, and Tubificidae. Although a microscopic flora is present in the bottom deposits, it was not included in this work.

Special attention was given to the microfauna of the profundal region, but collections have been made from all depths in the lake except the shoreward part of the littoral region. Few collections were made at less than 4 m. water depth.

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ANNOTATED LIST

In this list the following data will be indicated after the name of each animal: (1) General region occupied (abbreviations used are: *L*, littoral; *SL*, sublittoral; *P*, profundal); (2), depth of superimposed water; (3), type of bottom occupied; and (4), number of collections (indicated in parentheses).

PROTOZOA

Rhizopoda

1. *Amoeba proteus* Leidy (?) L.; 5 m.; Sand; (1)
2. *Chyphoderia ampulla* (Ehrenberg) L., SL.; 3-10 m.; Sand, (3)

Only those shelled Rhizopoda which showed pseudopodia have been recorded.

3. *Difflugia constricta* (Ehrenberg) L.; 8 m.; Sand; (1)

4. *Difflugia lobostoma* Leidy L.; 8 m.; Sand; (1)
5. *Difflugia acuminata* Ehrenberg P.; 21 m.; Muck; (1)
6. *Pelomyxa palustris* Greeff P.; 15-21 m.; Muck; (3)

The size of this species is remarkable. Specimens up to 1.3 by 1.0 mm. were found. The protoplasm was loaded with diatoms, fine sand and other particles. One specimen was found as deep as 7-8 cm. within the bottom deposits. This protozoan was never very numerous. It has been found in the absence of free oxygen.

7. *Pelomyxa villosa* Leidy P.; 14-23 m.; Muck; (15)

This amoeba is distinctly a profundal organism. It was found but once above 18 m. water depth. It was much more numerous below 19 m. than above this level (Table 3). In several instances it was present under anaerobic conditions.

Individuals of this species are not as large as those of the preceding one, the usual length being about 0.3-0.35 mm., the maximum length about 0.5 mm. Many specimens show the characteristic posterior bulb which is covered with numerous fine villi, 3-5 micra in length. This bulb is that part of the animal set off by a constriction near the posterior end. It disappears and reappears as the animal moves. Individuals seldom show pseudopodia. Movement of the protoplasm is easily observed. The central region is distinctly fluid and this fluid protoplasm flows forward within an outer cylinder of more solid material. As the fluid protoplasm reaches the anterior end it turns to either side and becomes part of the more solid material. Some individuals are in a rounded condition and lack the posterior bulb and villi. These rounded specimens show some movement and have been observed finally to take on the oblong shape and move about much more actively. The protoplasm is loaded with diatoms and numerous transparent (siliceous?) particles.

Mastigophora

8. Unidentified flagellates

Numerous small unidentified flagellates have been observed in the bottom deposits. In the quantitative work, these were unavoidably included with the minute ciliates but they make up a very small fraction of the total.

Infusoria

9. *Coleps hirtus* Nitzsch L., SL., P.; 3-22 m.; Sand, Muck; (39)

This small ciliate was widely distributed in Douglas Lake, and was very numerous. Where a separate tally was kept in the quantitative work it made up 20-50% of all the minute ciliates. It was present but never numerous in the deep bottom under severe stagnation conditions.

10. *Cothurnia* sp. SL., P.; 12-21 m.; Muck; (8)

Cothurnia sp. is an epizoon on both active and encysted (Plate II, Fig. 12) *Canthocamptus staphylinoides*.

11. *Glaucoma frontata* (Stokes) [*Dallasia frontata* Stokes]
L., SL.; 3-12 m.; Sand; (2)

12. *Dileptus gigas* Claparède and Lachmann
L., SL.; 3-12 m.; Sand, Muck; (7)

13. *Frontonia leucas* Ehrenberg
L., SL., P.; 3-22 m.; Sand, Muck; (28)

While this species was quite widely distributed in Douglas Lake, it was absent from the deeper bottom in late summer, although present there in early summer. It has been found in the upper portion of the oxygen-free zone. Its distribution was spotted. Occasionally it was very numerous (maximum 2520 per sq. dm.).

14. *Leucophrys patula* Ehrenberg L.; 3 m.; Sand; (1)

15. *Loxodes rostrum* (Müller) L., SL.; 1-13 m.; Sand, Muck; (18)

This ciliate was very common (maximum 1733 per sq. dm.).

16. *Prorodon* sp. L.; 8 m.; Sand; (1)

17. *Spathidium* sp. SL., P.; 14-21 m.; Sand, Muck; (2)

18. *Spirostomum ambiguum* Müller-Ehrenberg
L., SL., P.; 5-22 m.; Sand, Muck; (28)

This ciliate was widely distributed in the bottom deposits. It was common but never as numerous as *Frontonia leucas*. It has been found in the absence of free oxygen.

19. *Spirostomum teres* Claparède and Lachmann (?)
P.; 17 m.; Muck; (1)

20. *Stentor coeruleus* Ehrenberg
(L.), SL., P.; 5-22 m.; Muck, (Sand); (12)

This ciliate was usually found on the muck bottoms of the sub-littoral and profundal regions. Once it was taken at 5 m. water depth on sand bottom. It was fairly common at times (maximum 106 per sq. dm.).

21. *Stentor polymorphus* (Müller) L., SL.; 3-13 m.; Sand, Muck; (5)

This Stentor occurred sparingly in the littoral and sublittoral zone. It was not found in the profundal region.

22. *Urostyla* sp. L., SL.; 3-13 m.; Sand; (3)

23. Unidentified suctorian L.; 8 m.; Sand; (1)

This suctorian was found as an epizoon on two different specimens of *Cyclops agilis*. On one Cyclops several were attached to the first antennae and on the other specimen there were five fastened to one furcal spine.

HYDROZOA

1. *Pelmatohydra* sp. L.; 3-5 m.; Sand; (2)

No attempt was made to determine the species of hydra. Miller (1936) reported both *Pelmatohydra oligactis* (Pallas) and *P. pseudoligactis* Hyman from Douglas Lake.

RHABDOCOELA

1. *Dalyellia* spp. L., SL.; 3-12 m.; Sand, Muck; (10)

Due to limited material the writer was unable to send Dr. Hyman as many specimens as was desirable. Dr. Hyman finds that there are at least two species of Dalyellia, neither one corresponding to known species. She states in correspondence that one is rather close to *D. rossi.*

2. *Gyratrix hermaphroditus hermaphroditus* Ehrenberg
L., SL.; 3-14 m.; Sand, Muck; (27)

This species was the most common of the rhabdocoels found. Specimens observed in June, July and August contained eggs with developing embryos. The eggs were separate, transparent, and light brown to yellowish in color. From three to six eggs were observed in a specimen. In some instances the embryos were active within the egg membrane.

3. *Macrostomum* sp. L., SL.; 4-10 m.; Sand, Muck; (3)

According to information supplied by Dr. Hyman in correspondence, these specimens of Macrostomum appeared to have no sex organs and consequently could not be identified to species. She states that the flattened rear end suggests *M. appendiculatum* (Fabricius) but that it would be necessary to examine the penis stilette before final decision could be made.

4. *Mesostoma macropenis* Hyman
L., SL.; 4-10 m.; Sand, Muck; (4)

This is a new species described by Dr. Hyman from material furnished her by the author. (Hyman, 1939.)

5. *Microstomum* sp. L., SL.; 4-15 m.; Sand, Muck; (6)

Specimens of Microstomum always contained nematocysts, some having as many as 500-700. In one instance, a hydra was found in the same sample. They usually were collected on sand bottom, but two individuals were taken on muck bottom at 15 m. water depth, during the fall overturn.

The *Microstomum* sp. and the *Stenostomum* sp. listed below were identified by the writer.

6. *Stenostomum* sp. L., SL.; 4-13 m.; Sand, Muck; (6)

NEMATODA

1. Small unidentified nematodes*
L., SL., P.; 1.5-22 m.; Sand, Muck; (61)

These small nematodes were very abundant in the bottom deposits. They were widely distributed, occurring in most of the collections. They were found in reduced numbers in the deeper profundal deposits under severe stagnation conditions. Quantitative and seasonal distribution of the nematodes, as well as their vertical distribution within sand and muck bottoms is discussed later.

* Professor L. J. Thomas states in correspondence (September 24, 1939) that the nematodes sent him are all of the genus *Trilobus bastian* 1865. "Small unidentified nematodes" throughout the paper refers to this species.

ROTATORIA

Practically all of the rotifers listed below were limited to the littoral region. Mr. Frank J. Myers informed the writer, in correspondence, that, with one exception, the material sent to him consisted of common cosmopolitan rotifers. Synonyms, as given by Mr. Myers, are included in brackets.

1. *Aspelta beltista* Harring and Myers L.; 5 m.; Sand; (1)
2. *Cephalodella gibba* (Ehrenberg) [*Diaschiza gibba*] L.; 5 m.; Sand; (1)
3. *Cephalodella megalocephala* (Glasscott) [*Diaschiza megalocephala*] L.; 4-6 m.; Sand; (1)
4. *Conochilus* sp. L.; 8-10 m.; Sand; (1)
5. *Dicranophorus artamus* Harring and Myers L.; 5 m.; Sand; (1)
6. *Dicranophorus edestes* Harring and Myers L.; 5 m.; Sand; (1)
7. *Dicranophorus epicharis* Harring and Myers L.; 4-6 m.; Sand; (2)
8. *Dicranophorus rostratus* (Dixon-Nuttall and Freeman) L.; 5 m.; Sand; (1)
9. *Diplcuchlanis propatula* (Gosse) [*Diplois propatula*] L.; 4-6 m.; Sand; (1)
10. *Dissotrocha macrostyla* (Ehrenberg) [*Philodina macrostyla*] L., SL.; 4-14 m.; Sand, Muck; (9)

Dissotrocha macrostyla has both the crawling and swimming habit. The body, except for the head and foot, is covered with a layer of detritus. This species and the more abundant *Rotaria* spp. were the only rotifers found in the deeper sublittoral and the profundal bottoms.

11. *Diurella insignis* Herrick L.; 4-6 m.; Sand; (2)
12. *Diurella tigris* (Müller) L., SL.; 4-11 m.; Sand, Muck; (7)

D. tigris was common on sand bottom in the littoral region. Only once was it found below 8 m. and then on muck bottom.

13. *Euchlanis parva* Rousselet L.; 4-6 m.; Sand; (1)
14. *Keratella cochlearis* (Gosse) [*Anurea cochlearis*] L.; 4-6 m.; Sand; (1)

This species was also a common plankter in Douglas Lake.

15. *Lecane crepida* Harring L.; 5 m.; Sand; (1)
16. *Lecane flexilis* (Gosse) [*Cathypna flexilis*] L.; 5 m.; Sand; (1)
17. *Lecane mucronata* Harring and Myers L.; 5 m.; Sand; (1)

According to information furnished the writer by Mr. Frank J. Myers in correspondence, *Lecane mucronata* is in all probability a psammobiotic species, and has hitherto been found only in acid waters. The only specimen collected was notable for the relatively great length of the anterio-lateral spines. Mr. Myers has made a slide of this specimen and deposited it in the American Museum of Natural History.

18. *Lecane signifera* (Jennings) [*Cathypna signifera*] L.; 4-6 m.; Sand; (2)

19. *Mikrocodides chlaena* (Gosse) L.; 5 m.; Sand; (1)
20. *Macrochaetus subquadratus* Perty [*Polychaetus subquadratus*] L.; 5 m.; Sand; (1)
21. *Monostyla lunaris* (Ehrenberg) L.; 3-6 m.; Sand; (5)
22. *Mytilina ventralis reduncа* (Ehrenberg) [*Salpina ventralis*] L.; 4-6 m.; Sand; (1)
23. *Notholca striata acuminata* Ehrenberg L.; 4-6 m.; Sand; (1)
24. *Notommata cyrtopus* Gosse L.; 5 m.; Sand; (1)
25. *Rotaria rotatoria* (Pallas) [*Rotifer vulgaris*] L., SL., P.; 5-22 m.; Muck, Sand; (23)
26. *Rotaria tridens* (Montet) [*Rotifer tridens*]

Mr. Myers explained in correspondence that *Rotaria tridens* is near *R. rotatoria*. It has a jaw formula of 3 plus 3, instead of 2 plus 2; the head is somewhat larger; and the spurs are slightly longer and narrower.

Rotaria rotatoria and *R. tridens* were the only rotifers found in the profundal bottom. They occurred in the deeper profundal deposits during late summer under severe stagnation conditions. They were present during the fall overturn at 21 m. water depth in much greater numbers than during the summer.

One type of locomotion exhibited by these species of *Rotaria* is probably associated with their benthic habit. They creep through and over the ooze, with the corona pulled in, their body lengthening and shortening in a telescopic fashion. They can expand the corona and swim, but this type of locomotion is less common than the other.

27. *Scaridium longicaudum* (Müller) L.; 4-6 m.; Sand; (2)
28. *Trichotria tetractis* (Ehrenberg) [*Dinocharis tetractis*] L.; 3-5 m.; Sand; (2)

GASTROTRICHA

1. *Chaetonotus* sp. L., SL., P.; 2-21 m.; Muck, Sand; (26)

Chaetonoti were present but apparently never very numerous. They have been found in the profundal region in the absence of free oxygen. They were present in fairly large numbers at 21 m. during the fall overturn.

2. *Lepidoderma* sp.

This species was not found in Douglas Lake proper but was taken from the bottom deposits at the head of Maple River (the outlet of Douglas Lake) in 0.5 m. of water.

OLIGOCHAETA

1. *Acolosoma* sp. L.; 4-9 m.; Sand; (4)
2. *Chaetogaster* sp. L., SL.; 3-15 m.; Sand, Muck; (26)

Chaetogaster is the only one of the Naididae which was found on muck bottom in the sublittoral region. It was the most common of the smaller Oligochaeta present in the littoral.

3. *Naidium* sp. L., (SL.); 4-11 m.; Sand; (5)
4. *Nais communis* Piguet (?) L.; 4-9 m.; Sand; (4)
5. *Paranais* sp. L., SL.; 4-11 m.; Sand; (3)
6. *Pristina longiseta leidyi* Smith L.; 2-9 m.; Sand; (5)
7. *Slavina appendiculata* (d'Udekem) L.; 4-6 m.; Sand; (1)
8. *Stylaria lacustris* (L.) L.; 5 m.; Sand; (2)

CLADOCERA

1. *Alona quadrangularis* (O. F. Müller)
L., SL.; 3-15 m.; Sand, (Muck); (16)

Alona quadrangularis was one of the more common benthic Cladocera. It was mostly limited to the littoral region, having been found below 11 m. but once, during the fall overturn. Only twice was it found on muck bottom. Rawson (1930) reported this species in Lake Simcoe from bottom zones extending from 2-45 m. His observations were made in May and June.

This species with its large post-abdomen and small antennae (Plate II, Figs. 21, 22) is well adapted to life on the bottom. The powerful post-abdomen, with its large claws and basal spines, numerous strong serrate marginal denticles, as well as patches of weaker lateral spines (two rows on each side of post-abdomen), makes a very effective organ of locomotion.

Bigelow (1928) listed this species as belonging to the "associated ooze-film cenosis" of the "inshore bottom systasis." While it may not plow through the ooze, it certainly rests upon it and uses its post-abdomen for moving over its surface.

2. *Alona guttata* Sars L.; 3-5 m.; Sand; (2)

Bigelow (1928) recorded *Alona guttata* as belonging to both the "associated ooze-film cenosis" of the "inshore bottom systasis" and the "vegetation systasis."

3. *Bosmina* sp. SL.; 13-15 m.; Sand, Muck; (2)

It is probable that this species is a plankter and that its occurrence in the bottom population may be accidental.

4. *Camptocercus rectirostris* Schoedler L.; 3-6 m.; Sand; (3)

Rawson (1930) reported *Camptocercus rectirostris* from bottom zones extending from 2-20 m. Bigelow (1928) placed it with the "associated ooze-film cenosis."

Structural features (Plate II, Figs. 28, 29) seemingly associated with locomotor habits are as follows: antennae small; post-abdomen long, narrow, and armed with numerous serrate marginal denticles; claws long, each with one long basal spine and one row of smaller spines along proximal half of claw.

5. *Chydorus faviformis* Birge L.; 4-6 m.; Sand; (2)

Chydorus faviformis was listed by Bigelow (1928) as belonging to the "protected bay association, pelagic systasis, subsurface cenosis." Its occurrence on the bottom in Douglas Lake was probably accidental.

6. *Chydorus piger* Sars L., SL.; 4-15 m.; Sand, (Muck); (13)

Chydorus piger was common on sand bottom, being as numerous as was *Alona quadrangularis*. It was found on the muck bottom once, at a depth of 15 m. during the fall overturn.

The antennae are moderate in size; the post-abdomen not especially large; the claws moderate in length; and the post-abdomen bears 7-8 marginal spines concentrated at the lower posterior angle. *C. piger* has no outstanding modifications for life on the bottom.

7. *Daphnia longispina hyalina galeata* (Sars)
L., SL., P.; 8-21 m.; Sand, Muck; (5)

8. *Daphnia pulex parapulex retrocurva* (Forbes)
L., SL., P.; 5-18 m.; Sand, Muck; (4)

9. *Drepanothrix dentata* (Eurén) L., (SL); 4-11 m.; Sand; (12)

Bigelow (1928) designated *Drepanothrix dentata* as belonging to the "protected bay association, pelagic systasis, subsurface cenosis." In Douglas Lake, it must also be considered as belonging to the littoral benthic fauna.

This species (Plate II, Figs. 25, 26, 27) has a small post-abdomen which is provided with many small spines and a small claw. The antennae are stout and each of the two proximal segments of the lower, 3-segmented ramus bears a long stout seta. These setae are about as long as the antennae. They are directed posteriorly. These setae are effective as structures for pushing the animal over the surface of the ooze film.

10. *Ilyocryptus sordidus* (Liévin)
L., SL., P.; 6-21 m.; Muck, Sand; (4)

Ilyocryptus sordidus was not common in Douglas Lake during the periods studied, having been found only four times during the five summers. The very interesting adaptations of this species, as well as those of other species of Ilyocryptus, were discussed by Bigelow (1928) who listed this cladoceran as belonging to the "ooze-film cenosis, inshore bottom systasis." Rawson (1930) reported *Ilyocryptus* sp. from bottom zones extending from 2-45 m. depth. Hankó (1927) described a new species, *I. balatonicus*, from the bottom ooze (gyttja) of Lake Balaton, Hungary. He discussed in detail its adaptations to life in the bottom ooze.

The antennae are broad and powerful (Plate II, Fig. 30) and are used for plowing through the ooze film rather than for swimming. The post-abdomen (Plate II, Fig. 31) is large and is equipped with many spines. It is effective in helping to push the animal through the ooze. Retention, after molting, of the shell with its marginal setae results in the animal becoming covered with large amounts of debris.

11. *Latona setifera* (Müller) L., SL.; 4-11 m.; Sand, (Muck); (10)

Bigelow (1928) listed *Latona setifera* as belonging to the "associated ooze-film cenosis." It shows no particular adaptations to the bottom ooze. The post-abdomen is small. The antennae are short and fan-like, being covered

with many plumose setae. They are swimming organs but are also effective in pushing aside particles of debris.

12. *Leydigia quadrangularis* (Leydig)

L., SL.; 8-15 m.; Muck, Sand; (8)

Bigelow (1928) placed *Leydigia quadrangularis* in the "ooze-film cenosis." It is similar in appearance to *Alona quadrangularis*. The post-abdomen (Plate II, Figs. 23, 24) is larger, and armed with lateral movable spines rather than fixed marginal ones as in *A. quadrangularis*. In both, the antennae are so small that they have only a very limited use as swimming organs.

There was a distinct difference in distribution of these two species, *L. quadrangularis* being mostly confined to muck bottoms of the sublittoral, while *A. quadrangularis* is usually found on sand bottoms of the littoral region.

13. *Monospilus dispar* Sars L.; 4-6 m.; Sand; (1)

Only one specimen of *Monospilus dispar* was found (August, 1937). Shells of dead specimens were seen several times. Like Ilyocryptus, it retains the molted shell. The one specimen found was free of any covering of debris. The post-abdomen is powerful and armed with broad, strong claws. Bigelow (1928) indicated this species as belonging to the "ooze-film cenosis" and discussed its adaptations to the ooze-film.

14. *Ophryoxus gracilis* Sars L.; 4-10 m.; Sand; (4)

Bigelow (1928) indicated *Ophryoxus gracilis* as belonging to the "protected bay association, pelagic systasis, subsurface cenosis."

The antennae are weak; the post-abdomen stout, with a broad posterior margin; the distal posterior margins of the post-abdomen armed with nodules covered with fine hairs; and the claws long, with two basal spines. The post-abdomen is an effective organ for aiding locomotion over the ooze-film.

COPEPODA

1. *Attheyella illinoisensis* (Forbes) L.; Sand
2. *Attheyella northumbrica* (Brady) L.; Sand
3. *Bryocamptus hiemalis brevifurca* Coker L.; Sand

The three Harpacticidae just mentioned were lumped in the quantitative work. They were numerous on the sand of the littoral and upper sub-littoral regions, rarely being found on muck bottoms. They have been secured from 1.5-14 m. water depth in 28 collections.

4. *Canthocamptus staphylinoides* Pearse

Active animals L., SL., P.; 5-21 m.; Sand, Muck; (21)
Cysts L., SL., P.; 5-18.5 m.; Sand, Muck; (16)

This Canthocamptus was present both in an active and encysted condition (Plate III, Fig. 32) throughout the summer. The active individuals were not numerous during the early summer but increased in number as the season progressed due to excystment of encysted individuals. During the late sum-

mer active individuals were found at 17 and 18.5 m. water depth in the absence of free oxygen. Practically all had excysted (Fig. 8) by the last of October.

Active individuals of the summer population are full grown but sexually immature. During the fall overturn, the active animals showed reproductive activity. Many females carried egg cases; many pairs were copulating; and some females bore spermatophores.

Active individuals were distinctly benthic organisms, being able to move readily through the thin ooze by means of the feet and antennae.

The writer has found no previous record of cysts of *Canthocamptus* in North America. Lauterborn and Wolf (1909) reported cysts of *C. microstaphylinus* Wolf in Untersee, Germany, in June, from 15 to 20 m. water depth. Kessler (1912) found cysts of *Canthocamptus staphylinus* var. *thallwitzi* Kessler and of *C. microstaphylinus* in ponds in the vicinity of Dresden, Germany. He also reported the formation of cysts from active individuals of *C. staphylinus thallwitzi* under laboratory conditions. Dr. Edward S. Deevey, in a letter to Professor F. E. Eggleton of July 1, 1937, reported finding cysts of *C. staphylinoides* in several Connecticut situations in 1937.

Canthocamptus staphylinoides cysts (Plate III, Fig. 32) are flattened discs with a diameter of 0.42-0.55 mm. The thickness of the disc is about one-half its diameter. There are cysts of two sizes, the smaller ones containing males and the larger ones females. Within the cyst, the abdomen is bent dorsally over the cephalo-thorax. The cyst is composed of firm material which permeates and cements together particles of debris. Lauterborn and Wolf described the cysts of *C. microstaphylinus* as composed of two layers, a homogeneous inner one and an outer heterogeneous one, the cementing material alone forming the inner, while the cementing material with particles of debris formed the outer layer. This division of the cyst wall into two layers apparently does not hold for *C. staphylinoides*. The cyst is not attached to the animal, and the latter can turn round and round within the cyst. The animals can be shelled out of their cysts quite easily. In excystment, the animals escape through a hole in the side of the cyst which they apparently make by extending the abdomen and rupturing the cyst. Empty cysts retain the same form as before, and can be recognized in the bottom deposits. Encysted animals are full-grown and the sexes can be distinguished by means of the antennae.

Quantitative and seasonal distribution of the cysts, their vertical distribution in the bottom deposits, and the factors concerned in encystment and excystment are discussed later.

5. *Canthocamptus* sp. L., SL.; 1.5-13 m.; Sand; (8)

Regarding this species, Dr. Coker states in correspondence that it is apparently of an undescribed species, resembling *C. minutus* in many respects,

but differing markedly from it in that the female has but one well-developed caudal seta.

These animals are quite common throughout the summer. They are more numerous at 5 m. water depth than below this level. Several copulating pairs were observed during the last half of July. At that time, this species could be distinguished by two bright red lines, one on each side of the digestive tract, a character which did not show at other times.

6. *Cyclops bicuspidatus* Claus

Adults, active	P.; 15-21 m.; Muck; (3)
Immature, active	SL., P.; 11-22 m.; Muck, Sand; (12)
Cysts	P.; 15.5-22 m.; Muck; (20)

The encysted immature individuals (Plate III, Fig. 33) were present in enormous numbers throughout the summer. The number of cysts increased as the summer progressed (Fig. 9). In two instances, a single cyst was found at 11 m. water depth, in muck bottom. All other cysts were found at 15.5 m. water depth and below. Both adult and immature individuals are present in the plankton during the summer, being a common but not the predominant Cyclops. Adults of *C. bicuspidatus* were the predominant Cyclops of the plankton collected October 30; a few immature individuals were also present in this plankton.

Adult specimens of *C. bicuspidatus* were found but once in the bottom deposits. This was during the fall overturn. They are considered as accidental in the bottom population.

While the number of active immature individuals of *C. bicuspidatus* in the bottom deposits was small, they were more numerous than the adults. In many samples, no active individuals were present, while the cysts occurred in large numbers. In other samples, there were a few active individuals and many cysts. It is possible that some or all of these active individuals were present as encysted individuals and had excysted during the time between collection and examination of the sample.

Cysts of *Cyclops bicuspidatus* were reported by Birge and Juday (1908) from the bottom deposits of Lake Mendota and other Wisconsin lakes.

The cysts (Plate III, Fig. 33) of this Cyclops are ovoid: about 0.6 mm. long; and about 0.45 mm. in greatest diameter. Within the cyst, the abdomen is bent ventrally under the cephalo-thorax. The whole animal is apparently covered with some cementing substance which permeates and binds together particles from the bottom deposits. This coating of debris is firmly attached to the animal. Tips of the furcae and furcal spines extend through and beyond the cyst wall. When the animal excysts, there is no empty cyst, that can be recognized as such, left behind. When the cysts have been in surface lake water or in tap water for a time the animals, still covered with debris, can be seen extending and flexing the abdomen, and jerking the feet and antennae. After a few hours more, clean active Cyclops are present and there

is no trace of an empty cyst to be found. The animals in these cysts are all in the same stage of development. They are already in the "Cyclops" stage but are still sexually immature, and have 10-segmented antennae. Adults have 17-segmented antennae. The furca and fifth foot are like those of the adult. Excysted animals were reared to the adult condition and identified as *Cyclops bicuspidatus*.

Quantitative and seasonal distribution of the cysts, their vertical distribution in the bottom deposits, and the factors concerned in encystment and excystments are discussed later.

7. *Cyclops leuckarti* Claus L., SL., (P.); 5-21 m.; Sand, Muck; (16)

This Cyclops was found many times in the bottom deposits. It was not collected below 15.5 m. water depth during the summer, but was found at 21 m. during the fall overturn. This species has been taken from the bottom so many times that it can hardly be considered as accidental to the bottom population.

8. *Cyclops agilis* Koch, Sars [*Cyclops serrulatus* Fischer] L., SL., P.; 5-17 m.; Sand, Muck; (18)
9. *Cyclops viridis* (Jurine) L., SL.; 5-11 m.; Sand; (3)
10. Unidentified *Cyclops* (mostly immature) L., SL.; 2-15 m.; Sand, Muck; (17)
11. *Diaptomus* sp. L., SL., P.; 3-21 m.; Sand, Muck; (6)
12. Nauplii L., SL., (P); 3-21 m.; Sand, Muck; (21)

Nauplii were found in the profundal region only during the fall overturn but were fairly numerous in littoral and sub-littoral bottoms in summer. During the fall overturn, there was a very large population of nauplii at 15 m. water depth (2015 per sq. dm.). The fall overturn nauplii were possibly those of *Canthocamptus staphylinoides*, many females of which were found at that time bearing egg cases.

OSTRACODA

1. *Candona crogmaniana* Turner L., SL.; 4-12 m.; Sand, Muck; (6)

Specimens of this species were not as numerous as are those of the next two.

2. *Candona exilis* Furtos L., SL., P.; 4-18.5 m.; Muck, Sand; (27)
3. *Candona reflexa* Sharpe SL., P.; Muck. Sand

Candona exilis and *C. reflexa* were lumped in the quantitative work. Apparently, *C. exilis* was the more numerous of the two. Most of the records for these two species were from the sublittoral region. The quantitative series of July (Table 2) and of August (Table 3) show that they were most abundant in the sublittoral and upper profundal regions. These records also indicate that they were more numerous in muck than in sand bottoms at 11 m. water depth. A few individuals were found in August at 18.5 m. water depth in the absence of free oxygen. Quantitative and seasonal distribution of

Candona spp.. as well as vertical distribution in the bottom deposits, are discussed later.

Dr. Tressler states in correspondence that *Candona reflexa* is a very doubtful species and may, as Sharpe himself states, be only an immature stage of some larger species. It is the only Candona with the reflexed bristle on the third leg.

4. *Candona* (?) sp. SL.; 9-11 m.; Sand; (2)

Only four specimens of this animal were found. Three of them were dissected by the writer and one by Dr. Tressler who examined sketches of two of the specimens dissected by the writer and the slide made from the third. Dr. Tressler is convinced that it is an immature form, probably of some species of Candona. The first claw of the furca is about half as long as the second. The second claw is about two-thirds as long as the furca without the claws. The dorsal seta is about one-half the length of the furca without the claws. One specimen was 0.8 mm. long by 0.35 mm. high by 0.26 mm. wide.

5. *Cyclocypris serena* (Koch) L.; 4-9 m.; Sand; (3)

6. *Cypria exsculpta* (Fischer)
(L), SL., P.; 6-21 m.; Muck; Sand; (21)

7. *Cypria lacustris* Sars SL., P.; 9-22 m.; Muck, Sand; (24)

The two species of Cypria were not separated in the quantitative work. *C. lacustris* was somewhat more numerous. *Cypria* spp. were almost entirely confined to the sublittoral and profundal regions. They showed little difference in their distribution. It should be noted that these species occurred in considerable numbers in the deeper profundal region in late summer under severe stagnation conditions. Quantitative and seasonal distribution of *Cypria* spp., as well as vertical distribution in the bottom deposits are discussed later.

8. *Darwinula stevensoni* (Brady and Robertson)
L.; 4-9 m.; Sand; (3)

This interesting ostracod carries its young within the valves. About one-half of the specimens found were gravid. One female may contain five or six young, some of which are active.

In locomotion the first pair of antennae extends beyond the valves and are curved upward, while the second pair extends beyond the valves and curves downward and backward. The first pair serves to clear away debris while the second pair, working with the feet and furcae, functions in pulling the animal forward. This same arrangement and use of antennae have been noted for Candona and other ostracods.

9. *Limnicythere sancti-patricii* (Brady and Robertson)
L., (SL); 4-10.5 m.; Sand, (Muck); (10)

In one instance, this species was found on muck bottom at 10.5 m. water depth. Otherwise it was collected only on the sand bottom of the littoral region.

10. *Pionocypris obesa* (Brady and Robertson) L.; 4-9 m.; Sand; (5)
11. *Physocypria pustulosa* (Sharpe) SL.; 11 m.; Muck; (1)
12. Unidentified Ostracoda—small larval animals
L., SL.; 5-15 m.; Sand, Muck; (14)

ACARINA

The Hydracarina were all confined to the sand bottom of the littoral region. The oribatoidean (Horny water) mites and an unidentified mite, neither of which belongs to the Hydracarina, were the only species that were found on muck bottoms of the sublittoral region as well as in the littoral zone.

1. *Axonosis* sp. L.; 5-8 m.; Sand; (2)

Dr. Ruth Marshall indicated that this is an undescribed species. Two females were found.

2. *Forelia* sp. L.; 5-9 m.; Sand; (4)

This Forelia was also indicated as an undescribed species by Dr. Marshall. Three females and 5 nymphs occurred in the four collections.

3. *Koenikea marshallae* Viets L.; 5 m.; Sand; (1)
4. *Limnesia fulgida* Koch L.; 5 m.; Sand; (1)

Nymphs of *Limnesia* sp. were found in two other collections from 5 m. water depth. *Limnesia fulgida* was reported from Douglas Lake by Marshall (1927).

5. *Mideopsis* sp. L.; 5-9 m.; Sand; (3)

Dr. Marshall writes that the description of this species is in manuscript. She has several locality records of this species previous to this one.

6. *Mideopsis orbicularis* (Müller) L.; 5 m.; Sand; (1)

Marshall (1927) reported this species from Douglas Lake.

7. *Piona* sp. L.; 5-8 m.; Sand; (4)

Only nymphs of Piona were present in the collections sent to Dr. Marshall.

8. *Pionacercus* sp. L.; 8 m.; Sand; (1)

This form was also indicated as an undescribed species by Dr. Marshall. One female was found.

9. Nymphs of superfamily Oribatoidea
L., SL.; 3-14 m.; Sand, Muck; (9)

Dr. Ewing states in correspondence that there is no way of telling to what genus these mites belong without rearing them and that "our species" have never been reared.

This horny water mite was found more commonly on sand bottom. Three records were from the sublittoral region, one of these from muck bottom. They were never very numerous. The short legs and strongly curved claws enable it to move about quite easily in the ooze-film.

10. Unidentified mite* L., SL.; 5-15 m.; Sand, Muck; (8)

This species was the most common of the Acarina. Its legs are moderate

* Specimens of this mite have been sent to Dr. H. E. Ewing for identification.

in length. The terminal joint bears a pair of large sickle-shaped claws, very similar to those of the horny water mite. The animals move about quite readily among the ooze particles, clinging to larger fragments of plant remains and similar materials with their claws.

TARDIGRADA

1. *Macrobiotes* sp. L., SL.; 3-16 m.; Sand; (4)

These water-bears (0.2 mm.-0.3 mm. long), with their short legs and strongly curved claws, can cling very tenaciously to bits of debris and sand grains.

QUALITATIVE RELATIONS

Series of qualitative collections taken in 1935 and 1936 show several things regarding distribution up the slope of the basin during the summer stagnation period. As the depth within the hypolimnion increased, the number of species of microscopic benthic animals decreased. However, there are a few species which were able to maintain themselves in the deeper profundal bottoms under stagnation conditions which became increasingly severe. Not only did the number of species decrease with the increasing depth, but apparently there was a decrease in number of species at the same depth as summer progressed. Certain species, such as *Spirostomum ambiguum, Stentor coeruleus,* and *Frontonia leucas,* maintained themselves under anaerobic conditions for a shorter time than did others, such as *Coleps hirtus, Rotaria rotatoria,* and an unidentified nematode.

Qualitative sampling made it clear that during the summer the sand bottom of the littoral region supported a more diversified fauna than the muck bottom of the sublittoral and profundal regions. This was particularly true of the Rotatoria, Naididae, Cladocera, and Acarina. The Ostracoda were well represented in all regions of the lake, but the population of the littoral region was very different from that of the sublittoral and profundal regions. Except for *Canthocamptus staphylinoides,* the Harpacticidae were mostly limited to the sand bottom.

QUANTITATIVE RELATIONS

Table 1 summarizes four quantitative collections made during the last half of June, 1937. These collections were taken mainly for experimentation with methods of sectioning cores and methods of counting. Each collection consisted of a single core. Cores were sectioned at different levels to determine the most satisfactory method of dividing them into strata. The whole sample was counted without screening. Collections taken June 22 at 21 m. and June 30 at 6 m. water depth were counted immediately. The other samples, after being sectioned, were stored in a refrigerator for several days. This table is included because part of its data were used in graphing the seasonal distribution of certain organisms. A summary of the physico-chemi-

cal data of June 22 is as follows: Surface temperature, 21.4° C.; bottom temperature, 8.1° C. Thermocline, 9-14 m. O_2 at 16 m., 3.6 cc/l.; at 20 m., 0.07 cc/l. pH at surface, 8.2; of hypolimnion, 7.0. Free CO_2 at 16 m., 1.5 ppm.; at 20 m., 4 ppm.

Table 2 summarizes the results of a series of collections taken during July 1937. These collections were all made on transect AA except one taken July 20 at 11 m. water depth. This station, on transect BB, is about 250 m. south of transect AA, and was chosen in order to get a sample from muck bottom at this depth. The only apparent difference between the two stations was the type of bottom. Each collection was examined and counted before

TABLE 1. SUMMARY OF EARLY QUANTITATIVE SAMPLES TAKEN DURING JUNE, 1937. FIGURES GIVEN INDICATE THE NUMBER OF ORGANISMS PER SQUARE DECIMETER OF BOTTOM.

Date	6/22	6/30	6/22	6/30
Water depth in meters	21	15	11	6
Transect	AA	AA	AA	AA
Type of bottom	Muck	Muck	Sand	Sand
Area sampled in sq. cm.	3.8	3.8	3.8	3.8
Pelomyxa villosa	234	....	....	....
Pelomyxa palustris	....	26	....	....
Diffugia acuminata	52	....	....	....
Frontonia leucas	182	3120	....	26
Loxodes rostrum	....	....	....	52
Spirostomum ambiguum	1040	52	....	104
Stentor coeruleus	52	....	....	....
Minute ciliates	3172	1924	1482	1560
Nematoda	130	546	234	364
Stenostomum spp.	....	....	....	78
Unidentified Rhabdocoelida	....	....	....	26
Dissotrocha macrostyla	....	....	26	104
Rotaria spp.	130	....	....	....
Other Rotatoria	....	....	....	156
Chaetonotus sp.	26	....	....	26
Chaetogaster sp.	....	....	....	52
Alona quadrangularis	....	....	....	52
Bosmina sp.	....	26	....	....
Drepanothrix dentata	....	....	26	....
Ilyocryptus sordidus	....	....	....	26
Latona setifera	....	....	26	26
Leydigia quadrangularis	....	52	....	....
Canthocamptus sp.	....	....	....	156
Canthocamptus staphylinoides	....	....	130	....
C. staphylinoides (cysts)	....	832	....	....
Other Harpacticidæ	52	....	52	546
Cyclops bicuspidatus (immature)	572	....	....	....
Cyclops bicuspidatus (cysts)	7020	....	....	....
Cyclops agilis	....	26	104	26
Cyclops viridis	....	....	26	....
Cyclops sp. (immature)	....	78	....	26
Candona spp.	....	78	78	26
Cypria spp.	26	364	....	26
Ostracoda (immature)	....	....	130	104
Nauplii	....	....	52	52
Acarina	....	26	52	26
Macrobiotes sp.	....	....	....	52

the next was made. In most cases, a collection consisted of five cores. Physico-chemical conditions on July 16 are shown graphically in Fig. 2.

Table 3 summarizes a series of quantitative samples taken during the last half of August, 1937. These collections were all made on transect AA, except the one taken August 29 on muck bottom at 11 m. water depth. Three collections from sand bottom (11, 8 and 5 m.) were not examined alive. These

TABLE 2. SUMMARY OF A SERIES OF QUANTITATIVE SAMPLES TAKEN DURING JULY, 1937. FIGURES GIVEN INDICATE THE NUMBER OF ORGANISMS PER SQUARE DECIMETER OF BOTTOM.

Date	7/7	7/10	7/13	7/20	7/16	7/23	7/28
Water depth in meters	20	17	14	11	11	8	5
Transect	AA	AA	AA	BB	AA	AA	AA
Type of bottom	Muck	Muck	Muck	Muck	Sand	Sand	Sand
Area sampled in sq. cm.	11.4	19.0	19.0	19.0	15.2	19.0	19.0
Amoebaproteus	....	....	....	....	....	....	26
Dileptas gidas	....	....	....	....	....	....	26
Frontonia leucas	106	26	131	236	79	262	....
Loxodes rostrum	....	....	....	79	158	210	260
Spirostomum ambiguum	53	26	158	26	185	105	52
Stentor coeruleus	106	26	....	79	....	....	26
Stentor polymorphus	....	....	....	....	....	....	26
Minute ciliates	1478	4595	3780	4410	4673	4856	4568
Pelmatohydra sp.	....	....	....	....	....	....	5
Nematoda	176	2362	840	525	818	1129	630
Gyratrix h. hermaphroditus	....	....	10	5	20	....	21
Microstomum sp.	....	....	....	....	....	....	16
Unidentified Rhabdocoelida	....	....	....	....	....	....	21
Dissotrocha macrostyla	....	....	53	....	106	....	53
Rotaria spp.	53	26	....	....	....	53	53
Other Rotatoria	....	....	....	....	26	184	551
Chaetonotus sp.	....	53	....	....	53	78	525
Chaetogaster sp.	....	....	10	10	7	10	105
Other Naididae	....	....	....	....	....	5	....
Alona quadrangularis	....	....	....	....	7	26	5
Chydorus piger	....	....	....	....	....	10	58
Drepanothrix dentata	....	....	....	....	....	5	5
Latona setifera	....	....	....	....	7	10	....
Leydigia quadrangularis	....	....	5	....	7	....	....
Canthocamptus sp.	....	....	....	....	7	31	131
Canthocamptus staphylinoides	9	26	26	....	33	....	283
C. staphylinoides (cysts)	....	2772	1082	1937	205	5	10
Other Harpacticidae	9	....	....	....	46	84	84
Cyclops bicuspidatus (cysts)	6890	1811	....	5	....	....	....
Cyclops leuckarti	....	....	5	5	40	5	10
Cyclops agilis	....	5	16	....	13	37	....
Cyclops viridis	....	....	....	....	7	....	....
Cyclops sp. (immature)	....	5	37	5	13	....	16
Diaptomus sp.	....	....	....	....	....	....	37
Candona spp.	....	142	42	110	39	36	....
Cypria sp.	26	105	539	42	7	....	....
Darwinula stevensoni	....	....	....	....	....	21	....
Limnicythere sancti-patricii	....	....	....	....	....	....	47
Pionocypris obesa	....	....	....	....	....	....	5
Ostracoda (immature)	....	....	....	10	7	10	....
Nauplii	....	....	105	....	....	25	158
Acarina	....	....	5	5	13	36	42
Macrobiotes sp.	....	....	....	....	....	....	31

cores were sectioned and the aggregate samples screened with a 100-mesh Tyler screen, and the screenings preserved. Hence the Protozoa, Rhabdocoelida and Rotatoria could not be counted in these three samples. Physico-chemical conditions on August 22 are shown graphically in Fig. 3.

Table 4 summarizes two collections made during the fall overturn, October 30, 1937. The collections were examined immediately. Physico-chemical data of this date show the lake was homothermal at 7.0° C. Dissolved oxygen throughout the lake, 7.7 cc/l.; pH, 8.2; free CO_2, 0.0 ppm.

Examination of these summaries of quantitative series shows that during the summer: (1) Excluding the encysted *Cyclops bicuspidatus* and *Pelomyxa villosa*, both the number of individuals and the number of species decreased sharply in the deeper profundal region. (2) The sand bottoms of the littoral region supported a more numerous and more diversified fauna than did the

TABLE 3. SUMMARY OF A SERIES OF QUANTITATIVE SAMPLES TAKEN DURING AUGUST, 1937. FIGURES GIVEN INDICATE THE NUMBER OF ORGANISMS PER SQUARE DECIMETER OF BOTTOM.

Date	8/19	8/21	8/22	8/24	8/25	8/27	8/29	8/29	8/30	8/30
Water depth in meters	21.5	20	18.5	17	15.5	14	11	11	8	5
Transect	AA	AA	AA	AA	AA	AA	BB	AA	AA	AA
Type of bottom	Muck	Muck	Muck	Muck	Muck	Muck	Muck	Sand	Sand	Sand
Area sampled in sq. cm.	19.0	15.2	19.0	19.0	19.0	19.0	19.0	19.0	15.2	11.4
Pelomyxa villosa	265	442	131	....	....	....	....			
Pelomyxa palustris	....	....	53	....	....	....	....	The counts on		
Frontonia leucas	....	....	....	79	79	1496	2520	these three col-		
Loxodes rostrum	....	....	....	....	....	....	1733	lections were made		
Spirostomum ambiguum	....	26	131	....	26	52	....	from preserved		
Minute ciliates	184	390	1181	551	1129	2258	9030	screened samples.		
Nematoda	26	7	126	856	919	998	766	(100-mesh Tyler		
Stenostomum spp.	....	....	....	....	....	....	63	screen.)		
Gyratrix h. hermaphroditus	....	....	....	....	....	....	21			
Rotaria spp.	26	78	105	26	....	26	26	....	....	....
Other Rotatoria	....	....	....	....	....	....	52	....	....	....
Chaetonotus sp.	....	26	....	....	....	....	79	....	....	....
Chaetogaster sp.	....	....	....	....	....	5	5	....	7	44
Other Naididae	....	....	....	....	....	....	....	27	60	195
Alona quadrangularis	....	....	....	....	....	....	....	....	....	9
Chydorus piger	....	....	....	....	....	....	....	....	7	....
Daphnia longispina hyalina	....	....	....	....	....	....	....	5	13	....
Drepanothrix dentata	....	....	....	....	....	....	....	....	....	9
Ophryoxus gracilis	....	....	....	....	....	....	....	....	....	9
Canthocamptus staphylinoides	....	....	289	971	632	152	42	68	20	123
C. staphylinoides (cysts)	....	....	132	1228	1034	834	1250	116	....	....
Other Harpacticidae	....	....	....	....	....	....	....	....	33	132
Cyclops bicuspidatus (cysts)	13288	10296	4882	830	32	....	5	....	....	....
Cyclops leuckarti	....	....	....	....	26	52	16	11	13	....
Cyclops agilis	....	....	....	....	....	....	....	5	20	9
Cyclops sp. (immature)	....	....	....	....	5	5	11	....	....	....
Diaptomus sp.	....	....	....	....	5	....	....	5	....	35
Candona spp.	....	....	5	147	152	132	53	32	7	....
Cypria spp.	....	14	63	57	183	132	....	5	....	....
Pionocypris obesa	....	....	....	....	....	....	....	....	....	9
Ostracoda (immature)	....	....	....	....	....	5	....	....	....	9
Nauplii	....	....	....	....	....	26	26	....	....	....
Acarina	....	....	....	16	....	....	....	....	7	9

TABLE 4. SUMMARY OF TWO QUANTITATIVE SAMPLES TAKEN DURING THE FALL OVERTURN, 1937. FIGURES GIVEN INDICATE THE NUMBER OF ORGANISMS PER SQUARE DECIMETER OF BOTTOM.

Date	10/30	10/30
Water depth in meters	21	15
Transect	AA	AA
Type of bottom	Muck	Muck
Area sampled in sq. cm.	11.4	11.4
Pelomyxa villosa	528	....
Frontonia leucas	106	....
Stentor coeruleus	26	....
Minute ciliates	14626	6890
Nematoda	44	141
Microstomum sp.	....	18
Rotaria spp.	317	106
Other Rotatoria	....	106
Chaetonotus sp.	317	....
Chaetogaster sp.	....	9
Alona quadrangularis	....	26
Chydorus piger	....	18
Canthocamptus staphylinoides	18	2006
C. staphylinoides (cysts)	....	176
Other Harpacticidae	9	....
Cyclops bicuspidatus (adult)	18	9
Cyclops bicuspidatus (immature)	53	44
Cyclops bicuspidatus (cysts)	53	....
Cyclops leuckarti	9	26
Cyclops sp. (immature)	....	26
Diaptomus sp.	9	....
Candona spp.	....	9
Cypria spp.	....	18
Ostracoda (immature)	79	53
Nauplii	106	2015

muck bottoms of the sublittoral. Within the littoral region, the number of species and number of individuals were somewhat greater at 5 m. than at 8 m. water depth. (3) At the same depth, the fauna of the sand bottom was more numerous and more diversified than that of muck bottom (Table 2). With few exceptions, those species which were common to both situations were more numerous on sand bottom. Important exceptions are *Canthocamptus staphylinoides* cysts, *Candona* spp., and *Cypria* spp. A similar comparison is shown in Table 3. It is apparent that the type of bottom was a factor in determining the nature and amount of the microfauna.

DISTRIBUTION UP SLOPE OF LAKE BASIN

CANTHOCAMPTUS STAPHYLINOIDES (ACTIVE AND CYSTS) AND CYCLOPS BICUSPIDATUS (CYSTS)

Both of these copepods were found encysted in the bottom deposits. Differences in distribution of the cysts of these two species up the slope of the basin are shown in Figs. 2 and 3. In each figure, two collections made at 11 m. water depth are shown, one from sand and the other from muck bottom. All stations except one were located on transect AA. In order to

get a sample from muck bottom at 11 m. water depth, a station was selected on transect BB about 250 m. south of transect AA. Black bars represent the number of cysts of *Cyclops bicuspidatus* per square decimeter of bottom (approximately 16 sq. in.); cross-hatched bars indicate the number of *Canthocamptus staphylinoides* cysts per sq. dm.; and the open bars, the number of active *C. staphylinoides* per sq. dm.

The cysts of *Canthocamptus staphylinoides* were found from 11 m. water depth to 18.5 m. Very few cysts occurred above 11 m. water depth but this scarcity may be correlated not only with depth but also with the type of bottom. The only apparent difference between the two stations at 11 m. was in the character of the bottom. In muck bottom at 11 m. water depth there were about 10 times as many cysts as in sand bottom. The increase in the number of active *C. staphylinoides* and the decrease in the number of cysts in late summer should be noted although this is discussed under seasonal distribution.

Cyclops bicuspidatus cysts were found in large numbers at 17 m. water depth and below. A few cysts were collected at 15.5 m. water depth, and twice, a single cyst was found in samples from 11 m. An increase in the number of cysts with increasing depth was very definitely shown. The tre-

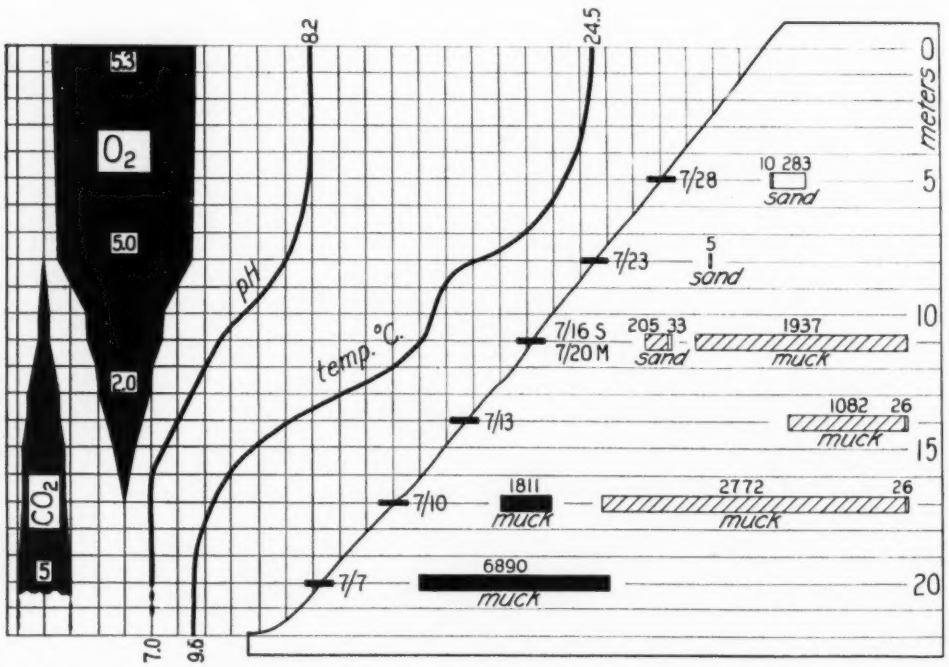

FIG. 2. Environmental factors and distribution up the slope of basin. Early summer, 1937. *Cyclops bicuspidatus* cysts (black bars), *Canthocamptus staphylinoides* cysts (cross-hatched bars), and active *C. staphylinoides* (open bars). The scale used in plotting the number of Canthocamptus is four times as large as the scale used for the number of Cyclops. The number of organisms per square decimeter of bottom, dates of collection, and type of bottom are indicated. Physico-chemical data: 7/16/37. Free CO_2 in ppm. O_2 in cc/l.

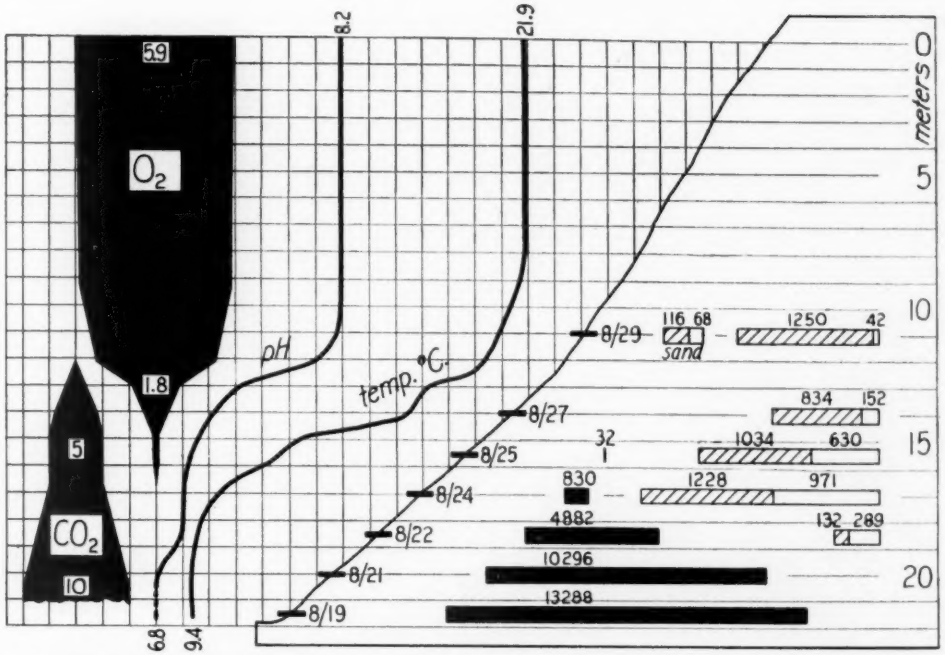

FIG. 3. Environmental factors and distribution up the slope of basin. Late summer, 1937. *Cyclops bicuspidatus* cysts (black bars), *Canthocamptus staphylinoides* cysts (cross-hatched bars), and active *C. staphylinoides* (open bars). The scales used are the same as those in Fig. 2. The number of organisms per sq. dm. of bottom, and dates of collection are indicated. All collections, except the one labeled sand, were made from muck bottom. Physico-chemical data: 8/22/37. Free CO_2 in ppm. O_2 in cc/l.

mendous population is apparent when it is realized that at 20 m. and below in late summer there are 1,000,000 to 1,300,000 per square meter of bottom. An increase in the number of cysts as summer progressed is indicated by a comparison of the two figures, but is more clearly shown in Fig. 9.

OSTRACODA

Distribution of the Ostracoda up the slope of the basin is shown in Figs. 4 and 5. In Fig. 4, two collections made at 11 m. water depth are shown. The black bars represent three species of *Candona: C. exilis, C. reflexa,* and *C. crogmaniana. C. exilis* made up the greater part of the population; *C. reflexa* was fairly common; and *C. crogmaniana* made up a very small fraction of the population. The cross-hatched bars represent *Cypria lacustris* and *Cypria exsculpta. C. lacustris* was somewhat more numerous than *C. exsculpta.* The open bars represent small immature ostracods that were found frequently. The stippled bars indicate other Ostracoda, namely *Limnicythere sancti-patricii, Pionocypris obesa,* and *Darwinula stevensoni.*

Figure 4 shows that the ostracod fauna of the littoral region was distinct from that of the sublittoral and profundal, with a certain amount of over-lapping in the case of *Candona* spp. Also, that at 11 m. the sand and

muck bottoms supported the same forms but that the sand bottom showed a much smaller population.

Both figures show a distinct concentration of Ostracoda at the bottom of the sublittoral region. Apparently, this concentration zone was more pronounced in early summer than in late summer. Also, while both Cypria and Candona persisted in the oxygen-free portion of the hypolimnion, Cypria extended farther into this region, indicating that it was able to withstand somewhat more severe stagnation conditions.

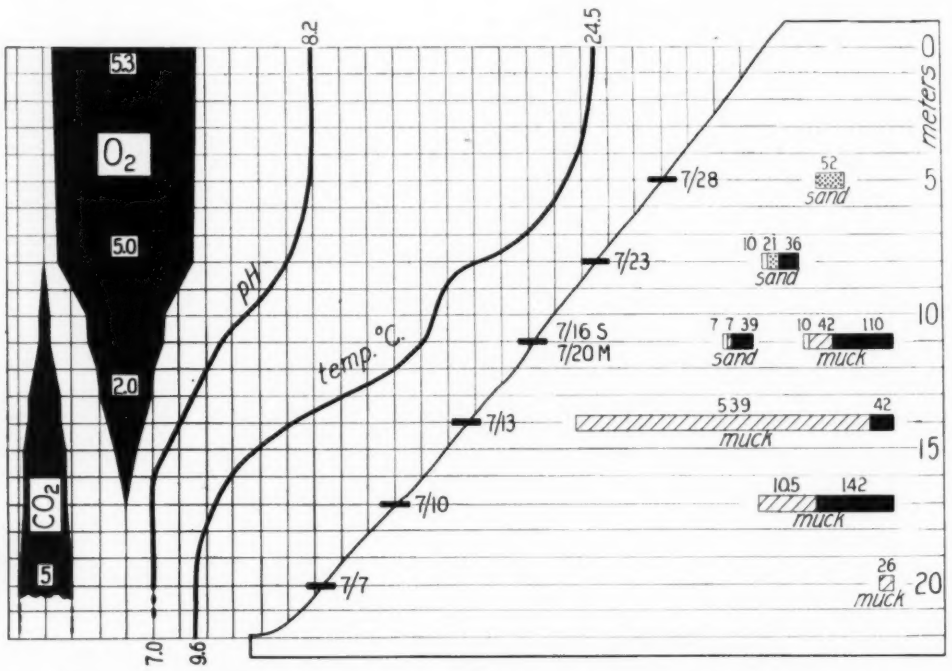

FIG. 4. Environmental factors and distribution up the slope of basin. Early summer, 1937. Ostracoda. (Black bars, *Candona* spp.; cross-hatched bars, *Cypria* spp.; open bars, small immature ostracods; stippled bars, other Ostracoda, i.e., *Limnicythere, Pionocypris, Darwinula.*) The scale used in plotting the number of ostracods is larger than those used in Figs. 2 and 3. The number of organisms per sq. dm. of bottom, dates of collection, and type of bottom are indicated. Physico-chemical data: 7/16/37. Free CO_2 in ppm. O_2 in cc/l.

NEMATODA

The distribution of the nematodes up the slope of the basin is shown in Figs. 6 and 7. The black bars represent the nematodes. In Fig. 6, two collections made at 11 m. water depth are shown.

Nematodes persisted into late summer in greatly reduced numbers in the oxygen-free portion of the hypolimnion. Fig. 6 shows a distinct concentration zone at about 17 m. This concentration zone did not appear in late summer (Fig. 7). No attempt is made to explain its presence early in the summer and its absence later.

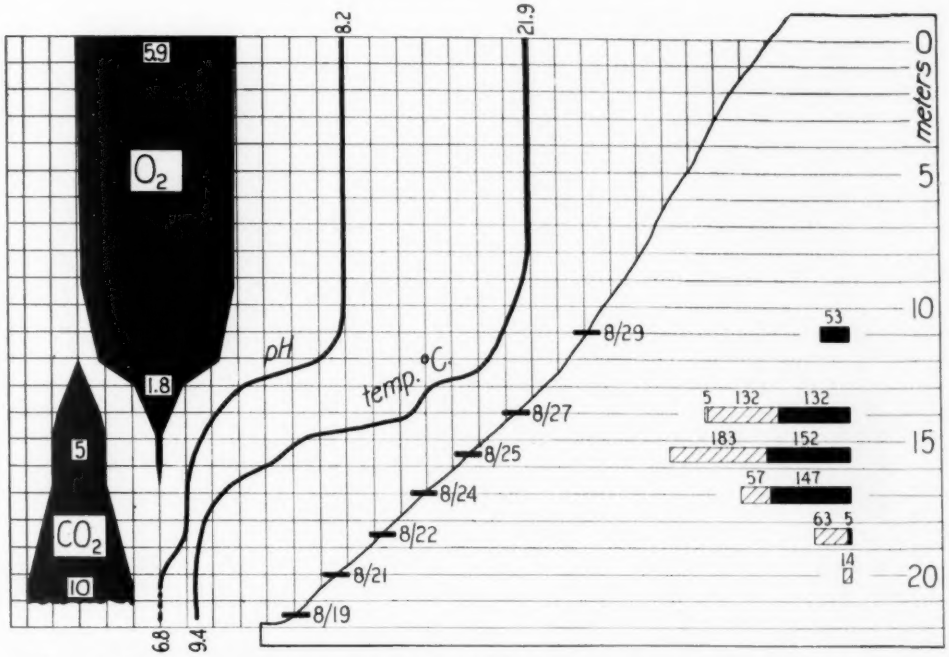

FIG. 5. Environmental factors and distribution up the slope of basin. Late summer, 1937. Ostracoda. (Black bars, *Candona* spp.; cross-hatched bars, *Cypria* spp.; open bars, small immature ostracods.) The scale used is the same as in Fig. 4. The number of organisms per sq. dm. of bottom and dates of collection are indicated. All collections were made from muck bottom. Physico-chemical data: 8/22/37. Free CO_2 in ppm. O_2 in cc/l.

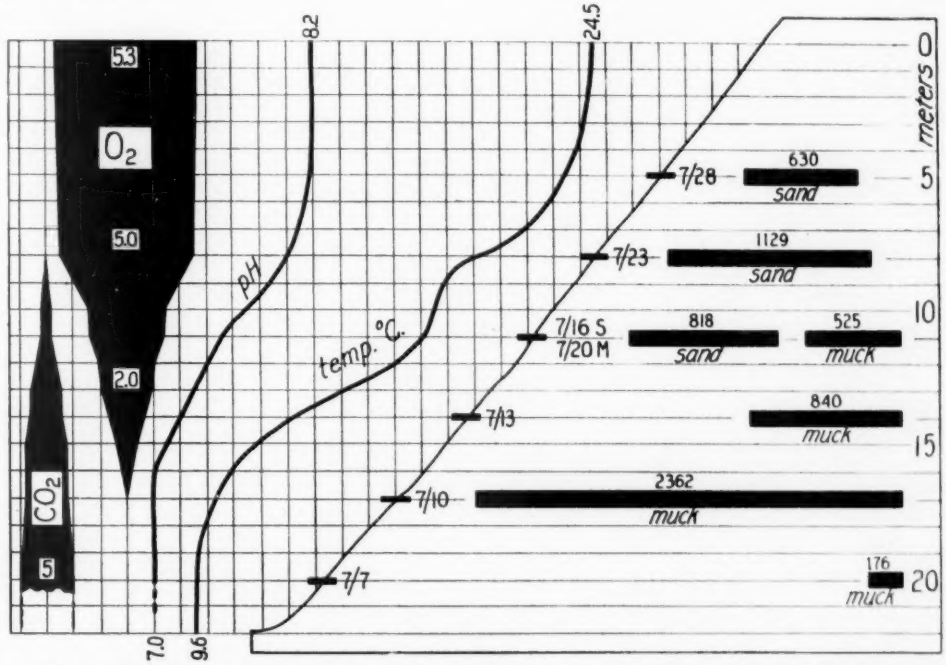

FIG. 6. Environmental factors and distribution up the slope of basin. Early summer, 1937. Nematoda. The scale used in plotting the number of nematodes is different from those used in Figs. 2, 3, 4, 5. The number of organisms per sq. dm. of bottom, dates of collection, and type of bottom are indicated. Physico-chemical data: 7/16/37. Free CO_2 in ppm. O_2 in cc/l.

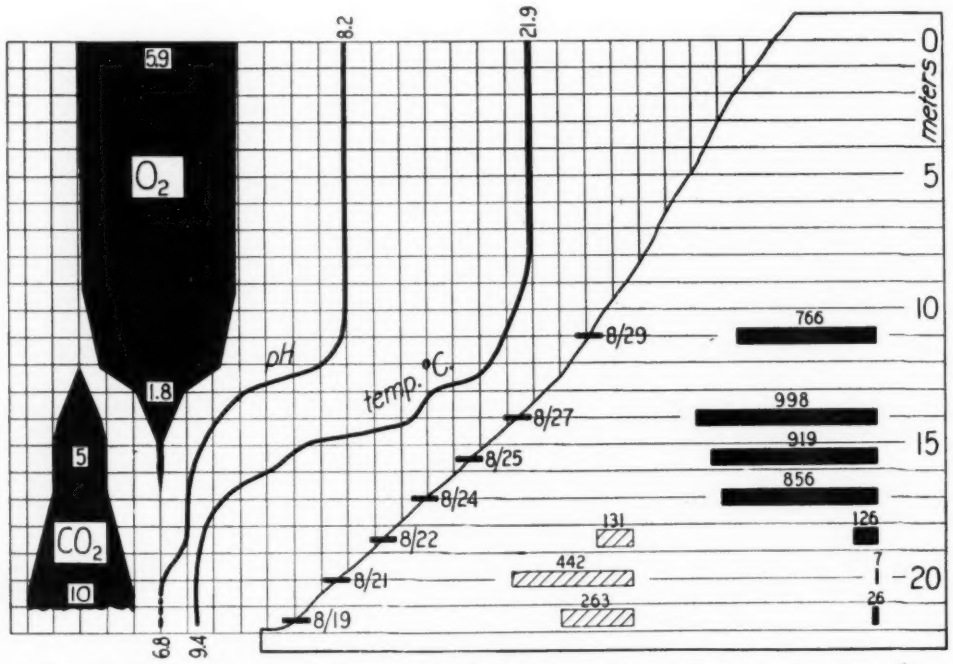

FIG. 7. Environmental factors and distribution up the slope of basin. Late summer, 1937. Nematoda (black bars) and *Pelomyxa villosa* (cross-hatched bars). The scale used in plotting the number of *Pelomyxa villosa* is 1.5 times as large as the scale used for the nematodes. The number of organisms per sq. dm. of bottom and dates of collection are indicated. All collections were made from muck bottom. Physico-chemical data: 8/22/37. Free CO_2 in ppm. O_2 in cc/l.

PELOMYXA VILLOSA

The distribution of *Pelomyxa villosa* is represented by the cross-hatched bars of Fig. 7. This animal was found but once above 18 m. water depth. It was present in large numbers in the deeper profundal region under severe stagnation conditions. It was present during the fall overturn at 21 m. in still greater numbers. (Table 4).

SEASONAL DISTRIBUTION (SUMMER AND FALL)

CANTHOCAMPTUS STAPHYLINOIDES (CYSTS AND ACTIVE)

Figure 8 shows the seasonal distribution of both encysted and active *Canthocamptus staphylinoides* in the muck bottom of the sublittoral and profundal regions. Cross-hatched bars represent encysted animals; open bars, active ones. The population was not a stationary one but rather there was a decrease in the number of cysts as summer progressed. Coincidently, the number of active individuals increased considerably. During the summer, active individuals showed no evidence of reproductive activity. These facts indicate that some of the animals excysted in mid-summer. Conditions during the fall overturn are shown by the collection made October 30, 1937. A few of the animals had not yet excysted. Active animals showed reproductive activity.

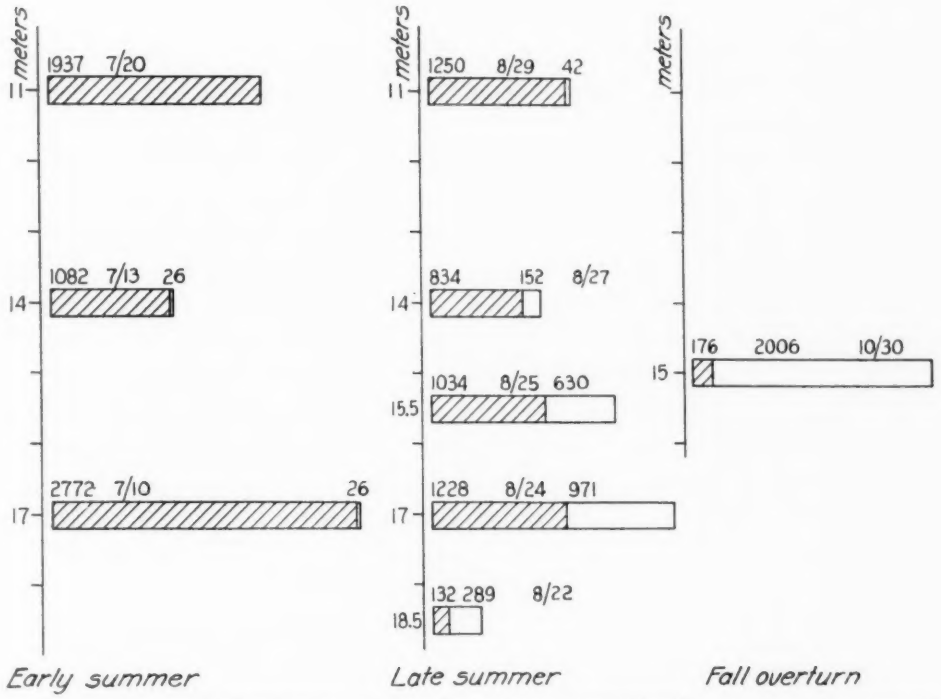

FIG. 8. Seasonal distribution of *Canthocamptus staphylinoides*, on muck bottom of sublittoral and profundal regions. 1937. Depth in meters, number of organisms per sq. dm. of bottom, and dates of collection are indicated. Cross-hatched bars represent cysts; open bars, active animals.

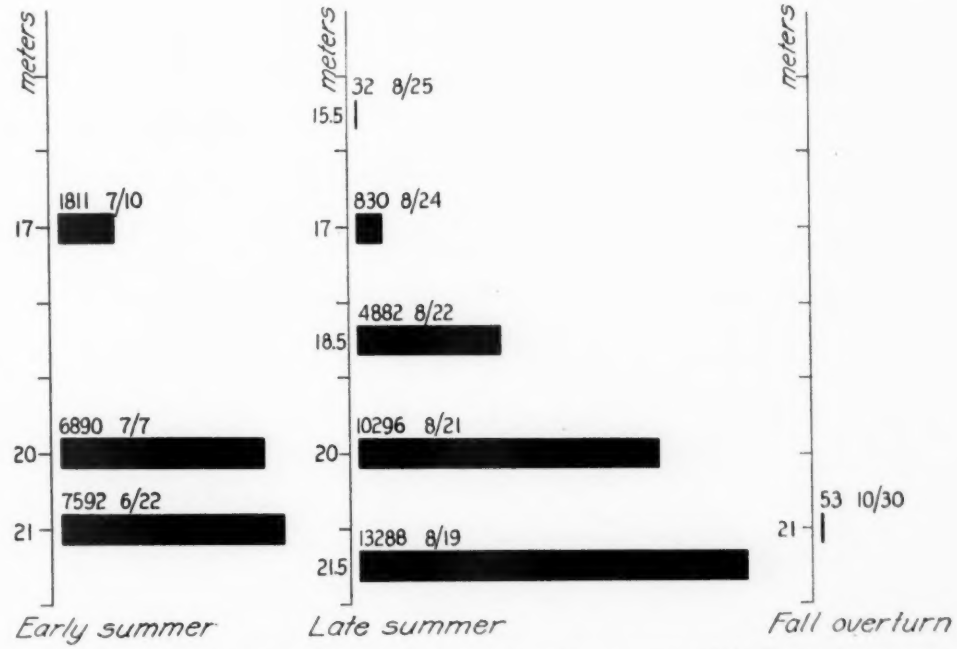

FIG. 9. Seasonal distribution of *Cyclops bicuspidatus* cysts. 1937. Depth in meters, number of cysts per sq. dm. of bottom, and dates of collection are indicated.

CYCLOPS BICUSPIDATUS (CYSTS)

Seasonal variations in the population of encysted *Cyclops bicuspidatus* are shown in Fig. 9. It should be noted that there was an increase in the number of cysts as summer progressed. Vertical plankton hauls made at various times during the summer showed that both adults and immature stages of *C. bicuspidatus* were present in moderate numbers. *C. bicuspidatus* is a plankter and throughout the summer apparently some of the immature individuals dropped to the bottom and encysted. Cysts had practically disappeared by October 30. The few that remained were in the 1-2 and 2-3 cm. strata. A vertical plankton haul made October 30 showed adult *C. bicuspidatus* to be the predominant Cyclops. No females with egg cases were noted, but several showed well-defined ovaries with eggs. Males were present, as well as a few immature individuals.

OSTRACODA

Seasonal distribution of Ostracoda in the sublittoral and profundal regions is shown in Fig. 10. Black bars represent *Candona* spp.; cross-hatched bars, *Cypria* spp.; open bars, small immature ostracods. The Cypria appear to

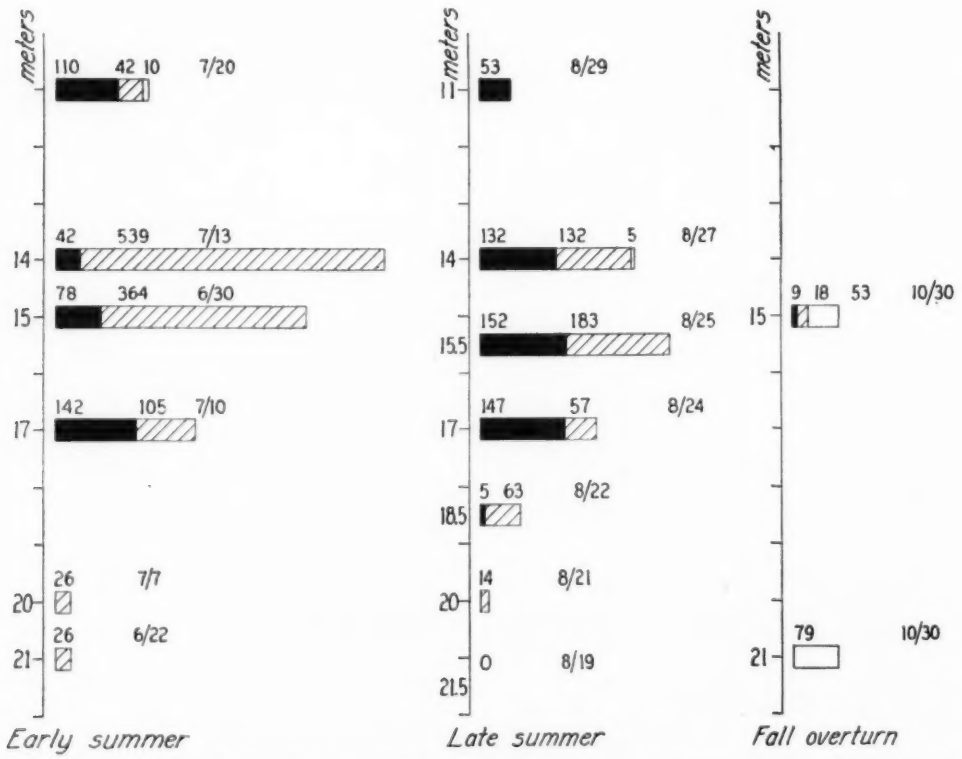

FIG. 10. Seasonal distribution of the Ostracoda on muck bottom of the sublittoral and profundal regions. 1937. Depth in meters, number of organisms per sq. dm. of bottom, and dates of collection are indicated. Black bars represent *Candona* spp.; cross-hatched bars, *Cypria* spp.; open bars, small immature ostracods.

have decreased in number from a spring or early summer maximum. This was not true of the Candona. Both groups had almost disappeared by the time of the fall overturn. The increase in number of small immature forms at the fall overturn should be noted. Observations extending throughout the entire year would probably furnish details of the life cycle needed to explain this variation in seasonal distribution.

NEMATODA

Figure 11 pictures the seasonal variations of the nematodes in muck bottoms of sublittoral and profundal regions. They decreased in number at 17 m. water depth and below from early to late summer; above that level, there appears to have been a slight increase in the population during the same period. While the fall series is very incomplete, it appears that the summer population had almost disappeared at that time. Again it is obvious that the complete story cannot be told without observations covering the entire year.

CILIATES

Figure 12 shows the seasonal variation of the total ciliate population on muck bottoms of the sublittoral and profundal regions. This group includes

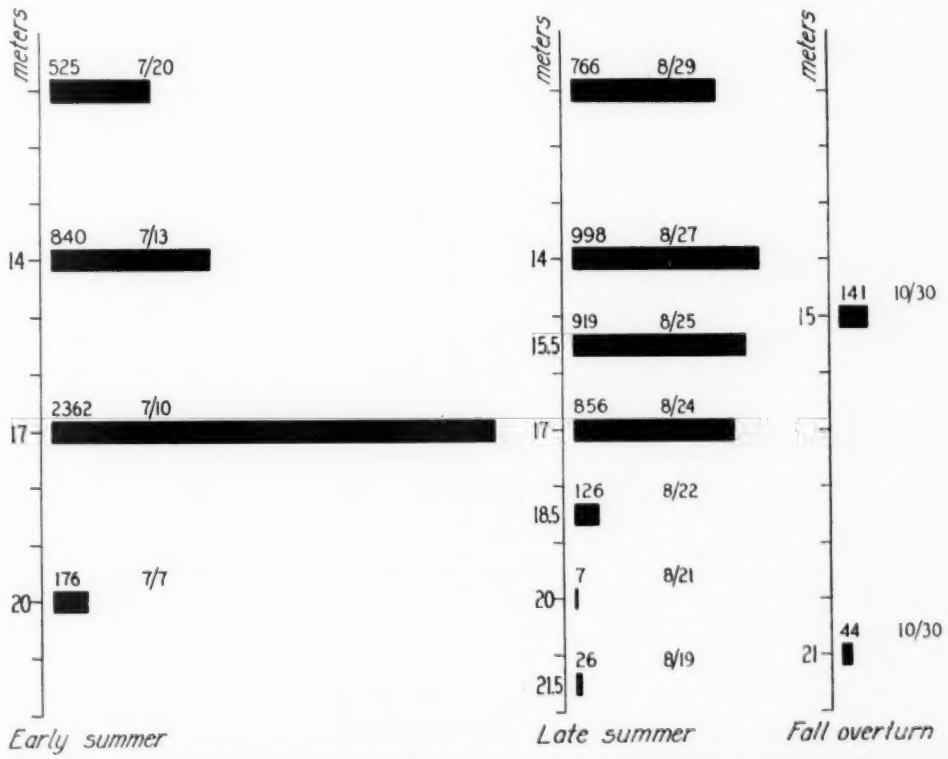

FIG. 11. Seasonal distribution of the nematodes on muck bottom of the sublittoral and profundal regions. 1937. Depth in meters, number of organisms per sq. dm. of bottom, and dates of collection are indicated.

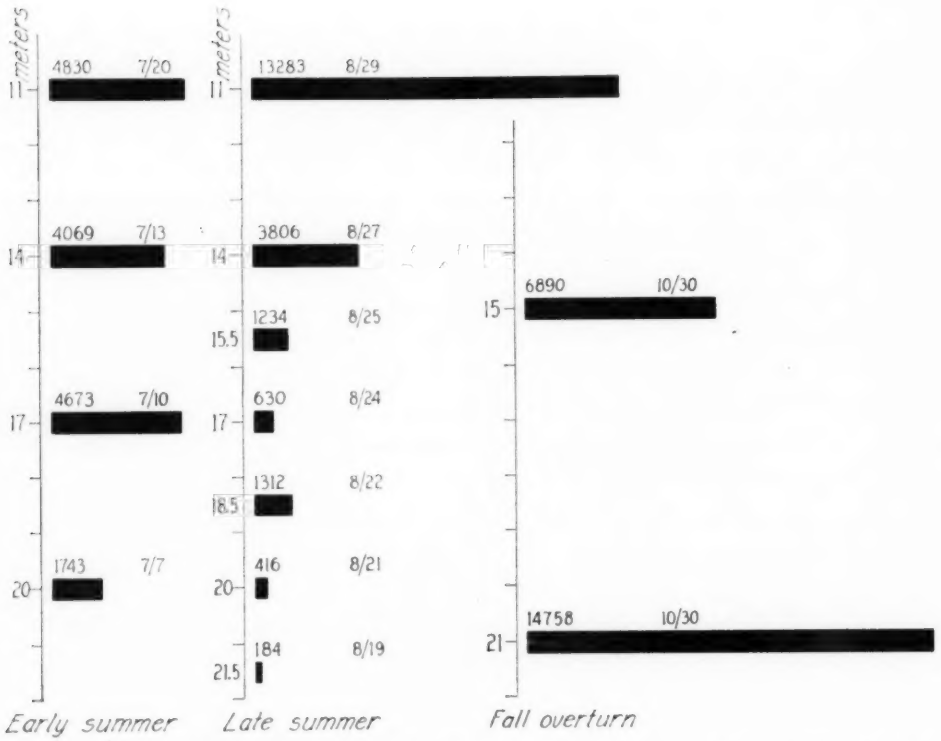

FIG. 12. Seasonal distribution of all ciliates on muck bottom of the sublittoral and profundal regions. 1937. Depth in meters, number of ciliates per sq. dm. of bottom, and dates of collection are indicated.

the minute, unidentified ciliates, as well as the following larger species: *Frontonia leucas, Loxodes rostrum, Spirostomum ambiguum,* and *Stentor coeruleus.* In each collection, minute ciliates made up the bulk of the population, except that in the collection at 14 m. water depth, August 27, 1937, Frontonia comprised about 40% of the total; and in the collection at 11 m., August 29, 1937, *Frontonia leucas* composed about 19%, *Loxodes rostrum* about 13%. Below 15 m. water depth there was a pronounced decrease in the number of ciliates as summer progressed. There was apparently a large increase in the population at 11 m. in late summer. The increase in the profundal region during the fall overturn should be noted. It is not possible to say how long the complete overturn had been in progress, but it was probably no longer than two or three weeks. Removal of stagnation conditions, and the short life cycle of the ciliates, would account for this more than 50-fold increase.

VERTICAL DISTRIBUTION IN BOTTOM DEPOSITS

Methods used in sectioning the cores made it possible to determine the level within the bottom deposits to which these microscopic organisms penetrated. Fig. 13 is a set of pictorial tables showing vertical distribution of

several organisms within the deposits. In these tables, each column represents a composite core of bottom deposits. The number of cores in each composite varied from 14 to 52. In each stratum is indicated the total number of organisms found in that stratum in all cores included. To facilitate comparison, the total number in all strata, as well as the number of cores, is given at the bottom of each column.

Figure 13 A shows the total number of cysts of *Cyclops bicuspidatus* in the various strata from 19 cores collected at 17-21.5 m. water depth, August 19-24, 1937. It should be noted that cysts were concentrated in the uppermost 2 cm. of the deposits and extended to the 5-8 cm. stratum.

The total number of cysts (Fig. 13 C) and of active individuals (Fig. 13 B) of *Canthocamptus staphylinoides* is indicated for the various strata from 20 cores at 11-17 m. water depth, August 24-29, 1937. It should be noted that the active individuals were concentrated in the first cm. of bottom deposits, while cysts were absent from the first 2 cm. and were concentrated in the 5-8 and 8-11 cm. strata. Concentration of the cysts in these strata can be explained most easily by assuming that Canthocamptus burrowed into the bottom deposits and then encysted.

Cypria spp. (Fig. 13 D) and *Candona* spp. (Fig. 13 E) showed striking differences in their vertical distribution. The numbers of *Cypria* spp. in the

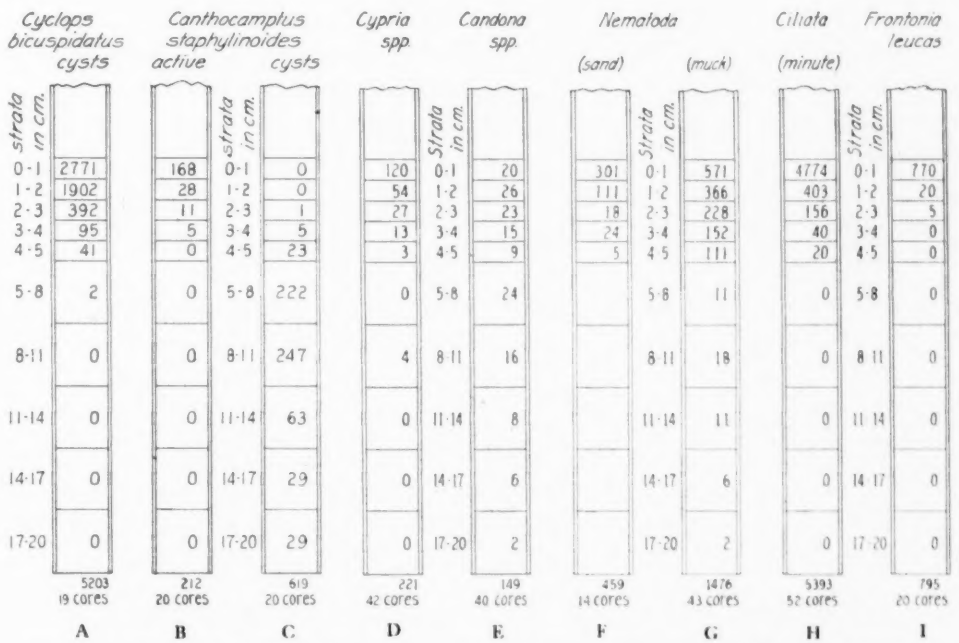

FIG. 13. Vertical distribution of several bottom organisms within the bottom deposits. Each column represents a composite core of the bottom deposits. The strata within the bottom deposits and the number of organisms found in each stratum are indicated. The number of cores used and the total number of organisms found are indicated below each column. All collections are from muck bottom except those summarized in column F.

various strata from 42 cores collected from 11-20 m. water depth, July 7-20 and August 21-27, 1937 are shown. The table for *Candona* spp. is based on 40 cores collected from 11-18.5 m. water depth, July 10-20 and August 22-29, 1937. All collections were from muck bottom. The Cypria were concentrated (55%) in the uppermost centimeter of deposits, and graded off sharply to the 3-4 cm. stratum, with only 3% of the total population below this level. The representatives of *Candona* spp., on the other hand, were about evenly distributed through the first 4 one-centimeter strata with 44% of the total population below the 4 cm. depth level. They extended into the 17-20 cm. stratum. This difference in distribution, or rather in burrowing habits, might be correlated with body form. Specimens of Cypria were high and narrow, the height of the valves being about 65% of the length, and the breadth of the animal 50 to 65% of its height. Specimens of *Candona exilis* as well as the other *Candona* spp. were low and broad, the height of the valves being slightly less than 50% of their length, and the breadth of the animal almost equaling the height. Possibly this latter body form is better suited for burrowing in the bottom deposits.

Distribution of Nematoda within sand bottom is shown in Fig. 13 F, which is based on 14 cores collected from 5-11 m. water depth, July 16-28, 1937. Their distribution in muck bottom is shown in Fig. 13 G, which is based on 43 cores collected from 11-20 m., July 7-20 and August 22-29, 1937. In sand bottoms, most of the nematodes were found in the first 2 cm. of the bottom deposits with 65% of the population in the uppermost cm. stratum. In muck bottom, about 38% of the population occurred in the uppermost cm. stratum. In this column (Fig. 13 G), the numbers of nematodes given for strata below 5 cm. are not high enough, since, as a rule, only screened samples were examined below this level. They do serve to show, however, that some nematodes lived as deep in the deposits as the 17-20 cm. stratum.

Figure 13 H shows the concentration of the minute ciliates near the surface of the deposits, with only 12% of the population below the 0-1 cm. stratum. This table is based on 52 cores, collected from muck bottom, 11-21.5 m. water depth, July 7-20, and August 19-29, 1937. Fig. 13 I showed for *Frontonia leucas*—one of the larger ciliates—a still more pronounced concentration near the surface of the deposits, with only 3% of the total population below the 0-1 cm. stratum. This table is based on 20 cores, collected from muck bottom, 11-17 m., August 24-29, 1937.

ENCYSTMENT OF *CYCLOPS BICUSPIDATUS*

Cysts of Cyclops bicuspidatus were reported by Birge and Juday (1908) from the bottom deposits of Lake Mendota and other Wisconsin lakes. They found them in very large numbers from June through September but more sparingly in October. They are reported here from the bottom deposits of

Douglas Lake. The fact that these cysts were found only in the profundal region and not over the whole bottom suggests that some factor, or factors, of the profundal waters served as a stimulus to which the animals react by encystment. That the absence of dissolved oxygen was not the causal factor was indicated by Birge and Juday. They found cysts early in the summer while the dissolved oxygen content of the profundal waters was still quite high (3-4 cc/l.). In the present investigation, no observations were made in late May and early June while the dissolved oxygen of the hypolimnion was plentiful. However, cysts have been found when the dissolved oxygen was low but not entirely depleted (0.1-0.5 cc/l).

The fact that the number of cysts in the bottom deposits increased during the summer and that both adult and immature *C. bicuspidatus* were present as plankters throughout the summer suggests that possibly this encysted period may be a life-history stage, i.e., when a certain stage of development is reached the immature Cyclops may settle to the bottom and encyst. But the fact that the cysts are confined to the deeper profundal bottom, increasing in number with increasing water depth, is hard to fit into this explanation.

Coker (1933) described some experiments with a *Cyclops* sp. from a marsh near Chapel Hill, North Carolina. Eggs of his *Cyclops* sp. develop normally only at low temperature. Nauplii, however, will continue their development at high temperature to the fourth copepodid stage, where their development is arrested. These *Cyclops* sp. remain active in this stage as long as 143 days, more than five times the period required from the egg to the fourth copepodid stage. Exposure to low temperature (6-8° C.) caused these arrested individuals to complete their development. It should be emphasized that this period of arrested development is not a resting period, the immature Cyclops remaining active.

It is possible that in *Cyclops bicuspidatus* we have an arrest of development combined with a resting (encysted) stage. The stimulus for encystment of the arrested immature Cyclops need not be high temperature or lack of dissolved oxygen. Any one factor, or a combination of several factors operative in the profundal waters might serve as a stimulus for encystment. That some factor in the profundal region is responsible seems likely since the cysts are confined to that region. No explanation is offered at this time as to the factors directly responsible for encystment.

The factors responsible for excystment are not known. A few cysts remained on October 30, 1937. They were not at the surface of the deposits but were in the 1-2 and 2-3 cm. strata. No observations were made between the last of August and October 30. Birge and Juday indicated that in Lake Mendota excystment occurs before the removal of stagnation conditions. They reported fewer cysts during the last half of September and still fewer in October, finding a single cyst as late as October 23. In this investigation, excystment was induced several times during the summer by placing the

cysts in surface lake water or in tap water for a few days. Some of the animals excysted within 24 hours while others took as long as 3 or 4 days.

The observations and experiments of Roy (1932) showing that adults and preadults of "*Diacyclops bicuspidatus*" Claus withstand desiccation of their habitat by the help of these protective envelopes, should be mentioned. Obviously, the encystment reported by Birge and Juday and by the present writer has no relation to desiccation, either as a factor responsible for encystment, or as an adaptation to the conditions of desiccation.

It should be pointed out that the release of these encysted Cyclops would result in a tremendous pulse of Cyclops in the fall plankton. Adult *Cyclops bicuspidatus* were the predominant Cyclops in the plankton collected October 30, 1937.

ENCYSTMENT OF *CANTHOCAMPTUS STAPHYLINOIDES*

Lauterborn and Wolf (1909) pointed out that *Canthocamptus microstaphylinus* is a winter species. They believed that there is but one generation a year and that the generation produced during the winter encysted when the water temperature rose above 12° C. and then excysted when it again dropped below 12° C. Excysted animals then became sexually active and produced the next generation. Donner (1928) discussed experimental work with *Canthocamptus staphylinus* from ditches which became dry during the summer. He believed his experiments indicated that encystment is a response to high temperature and not to drying. He showed that the encysted individuals cannot withstand complete desiccation.

The facts given in the present paper indicate that *Canthocamptus staphylinoides* is also a species reproducing only in winter. The temperature relations are, however, by no means as clear cut as those assumed by Lauterborn and Wolf for *C. microstaphylinus*. In Douglas Lake at 17 m. water depth, encystment (Fig. 2, 3) must have occurred in water no warmer than 10.5° C. At 18.5 m., there were a few cysts where the late summer temperature was 9.5° C. Also, in late summer, many of the animals had already excysted at 17 m. water depth where the temperature remained unchanged at 10.5° C. At 14 m., a smaller proportion of them had apparently excysted during the period when the temperature increased from 13° to 17.5° C. Obviously, considerable more investigation is necessary before any explanation as to the factors causing encystment and excystment of *Canthocamptus staphylinoides* can be offered.

INFLUENCE OF STAGNATION CONDITIONS

It seems profitable at this point to include by way of a summary a list of those microscopic bottom animals which have been found in Douglas Lake living under anaerobic conditions in the lower part of the hypolimnion. They are as follows:

Pelomyxa palustris
Pelomyxa villosa
Coleps hirtus
Cothurnia sp.
Frontonia leucas
Spirostomum ambiguum
Stentor coeruleus
Unidentified Nematoda
Rotaria rotatoria
Rotaria tridens
Chaetonotus sp.
Canthocamptus staphylinoides, cysts
Canthocamptus staphylinoides, active
Cyclops bicuspidatus, cysts
Candona exilis
Candona reflexa
Cypria exsculpta
Cypria lacustris

Except for the encysted *Cyclops bicuspidatus,* the only species occurring in considerable numbers in the deeper profundal region was *Pelomyxa villosa.* In late summer, *P. villosa* was confined to the oxygen-free zone of the hypolimnion. The other species listed above were found also in the upper part of the profundal, in the sublittoral, and to some extent, in the littoral region. Except for *Pelomyxa villosa* and encysted *Cyclops bicuspidatus,* these animals occurred in greatly reduced numbers in the lower part of the stagnation zone. It would seem that, barring the exceptions just mentioned, these organisms "endure rather than select an anaerobic environment" as Eggleton (1931) concluded in regard to the macroscopic profundal fauna. *Pelomyxa villosa* was found during the fall overturn at 21 m. water depth in much larger numbers than in August. This would indicate that it is also a facultative anaerobe.

SUMMARY

1. Special methods and apparatus for qualitative and quantitative investigation of the microscopic bottom fauna on sand and muck bottoms are described.

2. A total of 116 species of microscopic animals have been recorded from the bottom deposits of Douglas Lake, distributed in the following taxonomic groups: Protozoa, 23; Hydrozoa, 1; Rhabdocoela, 6; Nematoda, 1; Rotatoria, 28; Gastrotricha, 2; Oligochaeta, 8; Cladocera, 14; Copepoda, 11; Ostracoda, 11; Acarina, 10; Tardigrada, 1.

3. An annotated list of these microscopic benthic organisms which includes depth distribution, type of bottom in which they live, and the number of collections from which they were recorded, is presented.

4. Qualitative and quantitative studies show that: (a) A few species were able to maintain themselves in the deeper profundal bottoms under severe stagnation conditions. (b) Excluding encysted *Cyclops bicuspidatus* and *Pelomyxa villosa,* the microfauna decreased sharply in the deeper profundal region, both in number of species and number of individuals, during the summer stagnation period. (c) Certain species of microscopic benthic organisms were able to maintain themselves longer under anaerobic conditions than other species. (d) During the summer, sand bottoms of the littoral region supported a more diversified and a more numerous fauna than

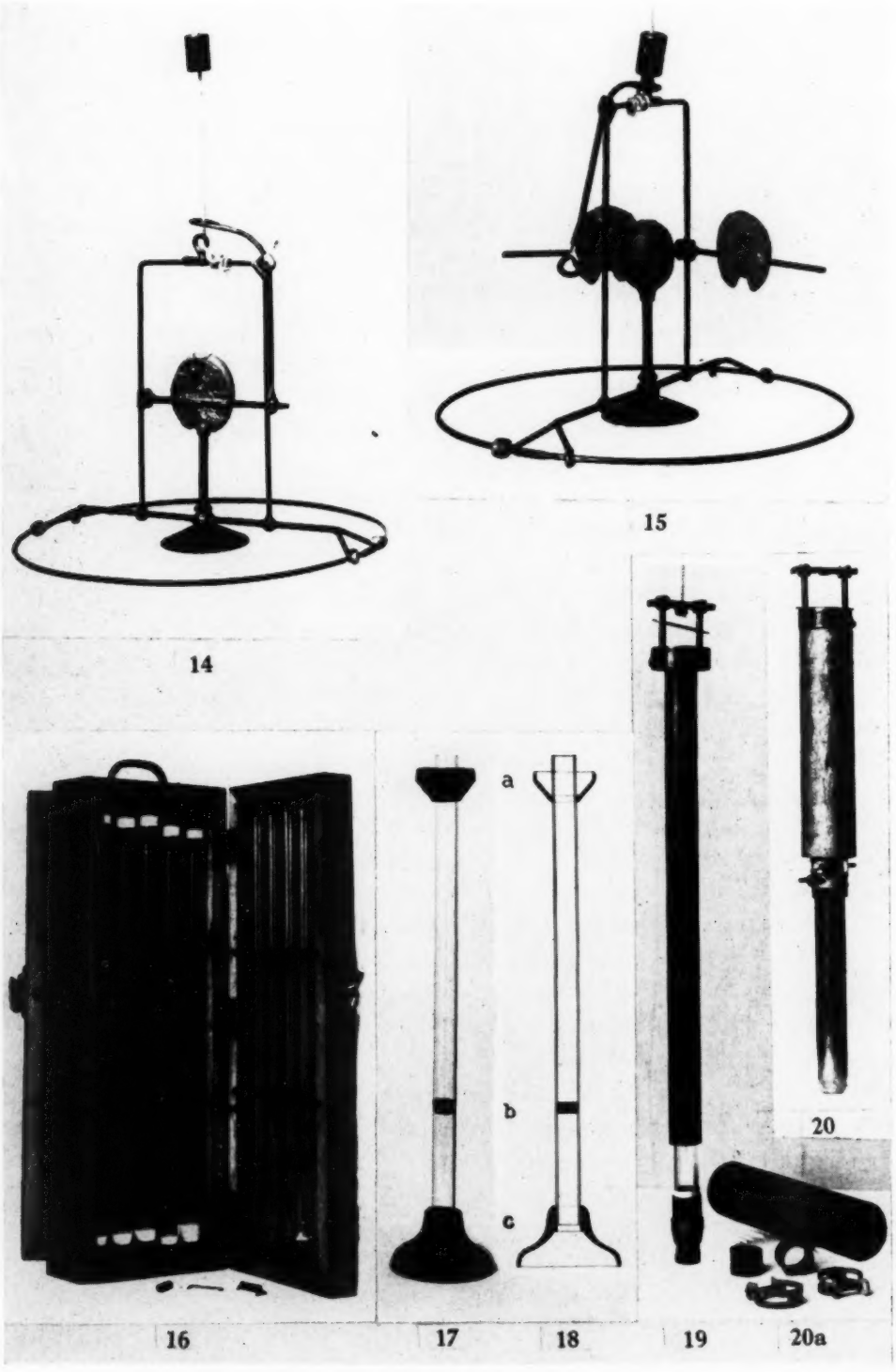

PLATE I

Apparatus used in a Limnological Investigation of Microscopic Bottom Fauna

FIG. 14. Ooze sucker before release. FIG. 15. Ooze sucker released. FIG. 16. Field case for extra glass tubes used in vertical core sampler. FIG. 17. Apparatus used in sectioning cores of bottom deposits. (a) Rubber cup. (b) Rubber piston. (c) Rubber base for holding glass tube. FIG. 18. Section of same. FIG. 19. Vertical core sampler with steel nose unscrewed showing glass tube. FIG. 20. Vertical core sampler loaded with heavy collar for use in sand bottom. FIG. 20a. Heavy collar and hose clamps used to attach same to vertical core sampler.

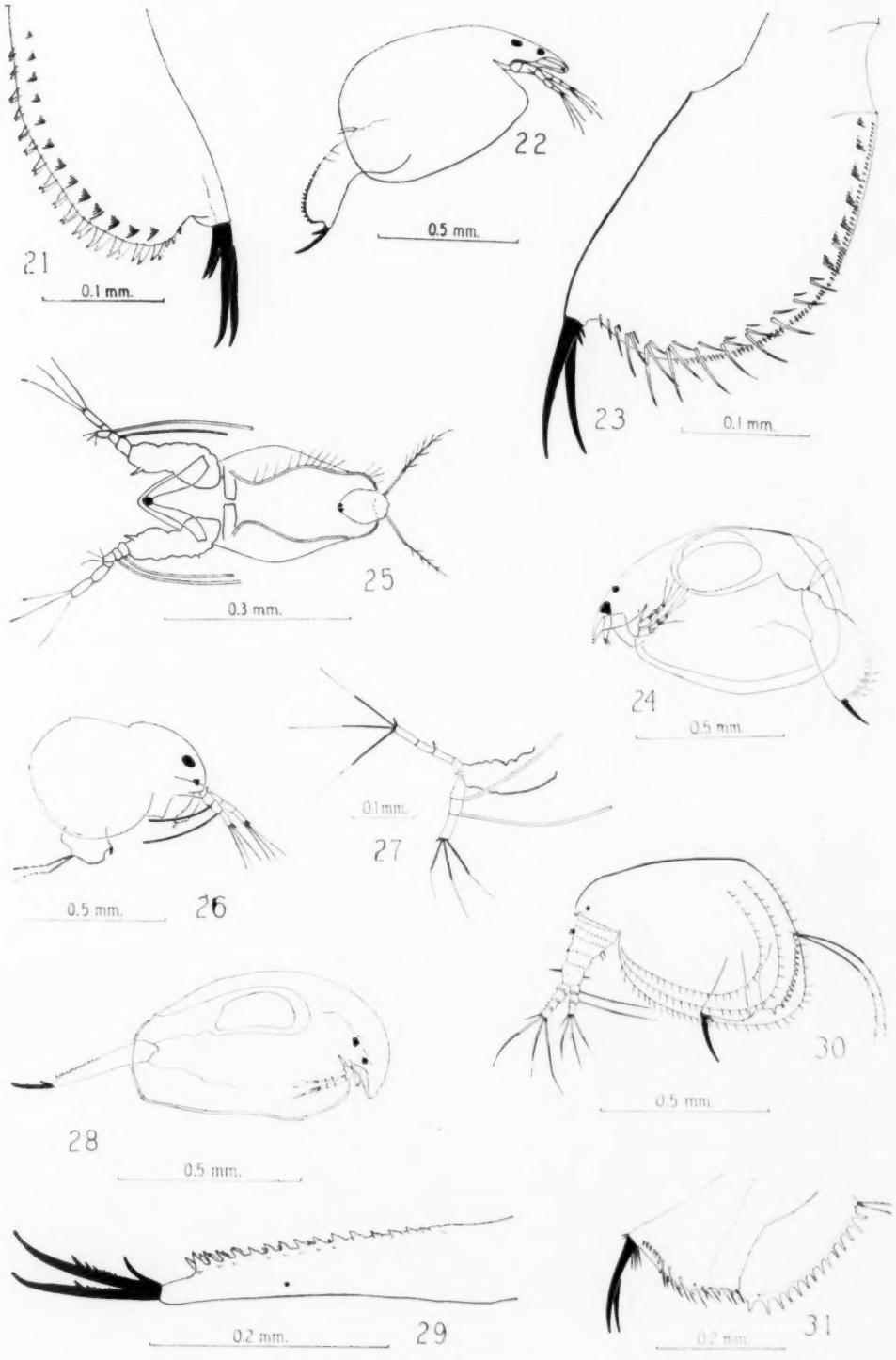

PLATE II

Cladocera from the Bottom Deposits of Douglas Lake

FIG. 21. *Alona quadrangularis*, post-abdomen. FIG. 22. *Alona quadrangularis*, side view. FIG. 23. *Leydigia quadrangularis*, post-abdomen. FIG. 24. *Leydigia quadrangularis*, side view. FIG. 25. *Drepanothrix dentata*, ventral view. FIG. 26. *Drepanothrix dentata*, side view. FIG. 27. *Drepanothrix dentata*, 2nd antenna. FIG. 28. *Camptocercus rectirostris*, side view. FIG. 29. *Camptocercus rectirostris*, post-abdomen. FIG. 30. *Ilyocryptus sordidus*, side view. FIG. 31. *Ilyocryptus sordidus*, post-abdomen.

FIG. 32

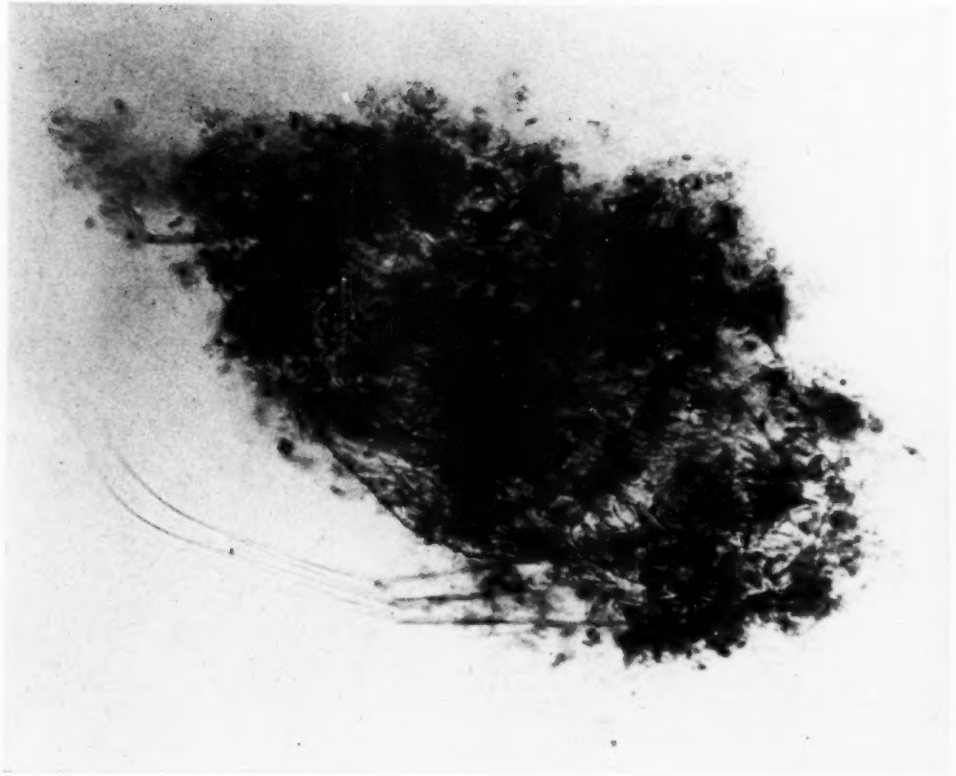

FIG. 33

PLATE III

FIG. 32. Cyst of *Canthocamptus staphylinoides*. Epizoic *Cothurnia* sp. attached to abdomen. Photomicrograph. x 165 diam. FIG. 33. Cyst of *Cyclops bicuspidatus*. Photomicrograph. x 165 diam.

did the muck bottoms of the sublittoral and profundal regions. (e) Within the littoral region the population increased to some extent with decreasing water depth both qualitatively and quantitatively. (f) The type of bottom was a factor in determining the nature and amount of the microfauna.

5. The relation of certain factors to the distribution up the slope of the lake basin is shown graphically for the following: *Canthocamptus staphylinoides,* cysts; active *C. staphylinoides; Cyclops bicuspidatus* cysts; Ostracoda; Nematoda; and *Pelomyxa villosa.*

6. The seasonal distribution throughout the summer and autumn is charted for the following: *Canthocamptus staphylinoides* cysts and active animals; *Cyclops bicuspidatus* cysts; Ostracoda; Nematoda; and Ciliata.

7. Microscopic benthic animals were by no means confined to the upper surface of the bottom deposits, certain of them penetrating at least to the 17-20 cm. stratum within the deposits.

8. Vertical distribution of different organisms within the bottom deposits varied considerably. Vertical distribution within muck bottoms is shown for the following: *Cyclops bicuspidatus* cysts; *Canthocamptus staphylinoides,* active and encysted animals; *Cypria* spp.; *Candona* spp.; Nematoda (both in sand and muck bottoms); Minute ciliates; and *Frontonia leucas.*

9. Encysted immature *Cyclops bicuspidatus* are reported from Douglas Lake where they are found in tremendous numbers in the profundal bottoms throughout the summer.

10. Encystment of full-grown but sexually immature *Canthocamptus staphylinoides* is reported from Douglas Lake. So far as the writer can determine, this is the first record of encysted *Canthocamptus* for North America.

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The Ecological Society of America

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AIMS

THE ECOLOGICAL SOCIETY OF AMERICA was founded in 1915 for the purpose of giving unity to the study of organisms in relation to environment, as a means of furthering intercourse between persons who are approaching widely different groups of organisms from closely related points of view, for the stimulation of ecological research, and to assist the development of the utilities which may be served by ecological principles.

MEMBERSHIP

Membership is open to those who are interested in the advancement of ecology or its applications, and to those who are engaged in any aspect of the study of organisms in relation to environment.

The following classes of membership are recognized:

Sustaining Life Members, minimum fee $200.00.

Life Members, fee $100.00. Funds obtained from the fees of both classes of Life Members are permanently invested.

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Three dollars of the dues received from active members, or of the interest in the case of Life Members of both classes, are applied as the annual subscription to ECOLOGY. Six dollars of the dues of Sustaining Members, and of the interest from the fees of Sustaining Life Members, are applied as the annual subscription to ECOLOGICAL MONOGRAPHS, the quarterly journal for longer articles. Members in arrears for dues will, on payment, be supplied with back numbers so far as they are available, but the journals do not hold themselves responsible for reserving back numbers in anticipation of the payment of back dues.

Associate members will be accepted for a single period of not more than three years with annual dues of $1.00. Such members do not receive ECOLOGY and are not eligible for office, but may become members in any one of the above classes upon the payment of the appropriate dues.

All members receive the BULLETIN OF THE ECOLOGICAL SOCIETY OF AMERICA, issued by the Secretary in March, June, October, and December. It contains announcements of meetings and excursions of the Society, abstracts of papers, programs, items of current interest to members, and occasional membership lists.

Checks should be made payable to Ecological Society of America. Application blanks for membership may be obtained from the Treasurer, to whom all correspondence regarding membership should be addressed.

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